

AN ABSTRACT OF THE THESIS OF

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Title: EFFECTS OF LIGHT, NUTRIENTS, AND GRAZERS ON PERIPHYTON
COMMUNITIES IN STREAMS

Abstract Approved:

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Relative effects of light, nutrients, and grazing on primary production were investigated in streams in the Cascade Mountains of Oregon and in laboratory streams. Relative magnitudes of primary production and associated processes were examined for one year in a stream that flowed through a clearcut and an old-growth forest in the Cascade Mountains.

Diel patterns of nutrients in four streams of different size indicated greater demand for inorganic nitrogen than phosphorus and suggested that uptake by aquatic primary producers was responsible for diel fluctuations of nutrient concentrations. Atomic ratios of N/P supported the conclusion that primary producers were most probably nitrogen limited.

In an experiment of light and nitrate addition to a stream in an old-growth forest, primary producer processes were enhanced by addition

of light (11000 lux) and by addition of both light and nitrate. There was no effect of nitrate addition on accumulation of algae, gross primary production, net community primary production, community respiration, P/R ratios, or community structure of diatoms at low ambient light levels (1100 lux). Addition of light resulted in greater colonization of algae, gross primary production, net community primary production, community respiration, P/R ratios and altered community structure of diatoms. The watershed was clearcut one year later and the experiment was essentially repeated with artificial shading instead of artificial lighting. Responses of colonization and primary production to light and nitrate in the clearcut were similar to those observed in the previous experiment in the old-growth forest.

Interactions between primary producers and grazers in lotic systems were examined in laboratory streams. Different densities of snails were established in laboratory channels; primary production in these channels was compared to production in a channel without grazers. Heavy and intermediate grazing resulted in decreases in standing crop of chlorophyll a, biomass/chlorophyll ratios, biomass of periphyton, gross primary production, and net community primary production. Low grazing densities did not significantly alter the above factors. Gross primary production increased with increasing standing crop of chlorophyll a but assimilation number was much greater at low standing crops; therefore, there was a partial compensatory mechanism for adjustment to grazing pressure. Total primary production was approximately equal at both high and intermediate densities of grazers

and was greater at low densities of grazers and no grazing. Taxonomic structure of periphyton was altered by heavy and intermediate grazing but not changed at low grazing pressures. Snail growth increased with increasing biomass of periphyton.

Responses of aquatic primary producers to canopy removal were examined in a clearcut and old-growth forest section of a stream in the Cascade Mountains of Oregon. Standing crop of chlorophyll a, biomass of periphyton, community respiration, assimilation number, and respiration per unit weight of periphyton were all significantly greater in the clearcut than in the old-growth forested section. Gross primary production was approximately 2.5 times greater in the open section than in the shaded section. Turnover times of periphyton were shorter in the clearcut than in the old-growth forest site. Photosynthetic efficiency was greater in the shaded site than in the open section. Processes of primary production were generally enhanced in the clearcut section of Mack Creek as compared to the old-growth forested section.

Shifts of food bases in streams from allochthonous material to autochthonous primary production may have major effects on structure and function of stream ecosystems. Succession of energy bases is best viewed in terms of overall watershed succession. Aquatic primary producers are an integral component of stream ecosystems and a major determinant of the nature and dynamics of higher trophic levels in streams.

Effects of Light, Nutrients, and Grazing
on Periphyton Communities in Streams

by

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Typed by Cheryl E. Curb for Stanley Vincent Gregory

Men have long been drawn to rivers,
Long before history,
Long before memory.

It is not by chance
That men find peace
In the whispers of a stream.

ACKNOWLEDGEMENTS

Many people have offered assistance, guidance, and encouragement during my graduate education. If I tried to thank everyone that helped, I would only succeed in failing. Therefore, I would like to offer my thanks to all who have given time, help, and ideas.

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I am deeply indebted to those involved in the development of the International Biological Program, a program based on the interaction of scientists from a wide array of disciplines. This experiment in research approaches firmly demonstrated that our ideas are products of group processes and are rarely, if ever, independently derived by single individuals. The original leaders of the Stream Team - Jim Hall, Norm Anderson, Jack Lyford, Jack Donaldson, Dave McIntire, Jim Sedell, and later, Frank Triska - gave me a chance and provided invaluable guidance throughout my graduate education. During the last of my education, Ken Cummins joined this list of eminent stream ecologists and greatly added to the perspective of the group. I was fortunate to be in a position to learn from these men.

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up on me. I must admit that he grayed considerably in the process. I have no idea why he had the patience to stick with me, but for whatever reason I owe Jim a great debt of gratitude.

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Lastly but most importantly, I want to thank my wife, Vicki. She not only put up with the hassles of being the wife of a graduate student, a fate worse than death, but she also remained my rock of support throughout the many frustrations and failures. She had to put up with P/R chambers littered all over the house, plexiglass shavings covering the living room, the smell of silacone sealant in her clothes, and endless last minute scrambles to get everything ready for research trips. She helped in the field and even took over sampling when I had to be away. Though I get to stick the title on the end of my name, this Ph.D. was earned as much by her as by me.

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EFFECTS OF LIGHT, NUTRIENTS, AND GRAZING ON PERIPHYTON COMMUNITIES IN STREAMS

INTRODUCTION

Watersheds of North America have been altered with increasing rapidity throughout the last 200 years. Most of these changes have involved removal of riparian vegetation, directly affecting sources of organic matter for stream ecosystems. Removal of terrestrial vegetation immediately alters the input of allochthonous detritus to a stream. Loss of canopy, however, may increase primary production in the stream by algae, moss, or macrophytes. Reduction of terrestrial vegetation also alters nutrient cycles within a watershed. In the Pacific Northwest, for example, output of nitrate from watersheds increases substantially after clearcutting (Fredriksen 1970). Elevated nutrient concentrations in such watersheds may stimulate aquatic primary production.

Faced with rapidly changing landscapes, man must know how ecosystems will respond to manipulations. Changes in stream ecosystems as a result of vegetation alteration will not be restricted to primary food sources. Shifts in relative inputs of allochthonous and autochthonous organic matter potentially influence community structure of benthic invertebrates, processing rates of organic matter, and productivity of different biotic components of streams. Responses to changes in the sources of organic inputs are functions of different physical, chemical, and biological characteristics of the material. Particle size and total quantity of available material differ between

the two food sources. Nitrogen content and lignification are greatly different in these forms of organic matter. Timing of inputs and availability of allochthonous and autochthonous organic matter are not alike. Retention, storage, and recovery patterns of the two food sources are dissimilar. A shift in the relative contributions of allochthonous and autochthonous food sources can be a major determinant of the structure and productivity of a stream system because of the disparity in the nature of these materials.

Timber harvest, a major land-use practice in the Pacific Northwest, abruptly alters streamside vegetation and potentially changes the basic food resources in streams. Decreased input of allochthonous organic matter is an obvious result of clearcutting. There is also a potential for enhancement of aquatic primary production as a result of increased solar radiation reaching the stream. Responses of primary producers in streams after clearcutting have been examined in only two previous studies (Hansmann 1969, Stockner and Shortreed 1976). Rates of primary production or algal accumulation in clearcut watersheds were just slightly greater than in old-growth forested watersheds in these studies. The lack of greater responses of primary producers is surprising in view of the tremendous change in environmental factors. Further investigation of the effects of canopy removal on primary production in streams in conjunction with studies of specific factors that may affect rates of primary production is needed to understand patterns of autochthonous production in streams of the Pacific Northwest.

Research in the International Biological Program in the Coniferous Biome provided an opportunity to examine the response of primary

producers to canopy removal and to evaluate the impact of that change on the rest of the stream community. In addition to my studies on primary production, other researchers examined litter decomposition, standing crops and emergence of aquatic insects, standing crops of trout and salamanders, and trout growth rates in the stream. Therefore, we were able to interpret changes in the aquatic biota in terms of the response of the stream community rather than just the response of particular organisms to clearcutting.

The goals of my research were to determine the relative magnitudes of primary production in an open and forested stream of the Cascade Mountains and to determine the relative effects of light, nutrients, and grazers on primary production in streams. These findings were then placed in the broader context of contribution of autochthonous primary production to the food resources of higher trophic groups in comparison to allochthonous contributions. The first two goals were approached by the following objectives:

1. Examination of the response of algal production in an old-growth forested stream to an increase in concentration of a critical nutrient and determination of the degree to which light affects such a response.
2. Determination of the impact of grazing pressure on primary producers in lotic ecosystems.
3. Estimation of primary production, standing crops of algae, and drift of algae in a third-order, mountain stream in an old-growth and clearcut section of the same watershed.

The latter goal of this research was addressed through the integration of the research with concurrent investigations by research personnel of the International Biological Program.

Study Areas

Light - Nutrient Relationships

Diel nutrient changes were observed in several streams in the H. J. Andrews Experimental Forest to provide information on potentially critical nutrients for primary production. Four principle sites were studied: Watershed 10 (WS 10), the old-growth forest section of Mack Creek (MF), the clearcut section of Mack Creek (MC), and Lookout Creek (LO).

Watershed 10 is a 10.2 ha watershed adjacent to the H. J. Andrews Experimental Forest. Dominant vegetation in WS 10 was a 450 year-old stand of Douglas-fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla). The stream in WS 10 is a first-order channel with a 45% gradient. The longitudinal profile of the stream consisted of a series of "stairsteps" created by debris dams that supported terraces of loose inorganic substrates. These debris dams were frequently connected by moss covered bedrock chutes. Rock substrates were derived from weathered volcanic tuff and breccia material. Streamflows ranged from 0.2 l/sec in summer to 67.3 l/sec during the study period.

During the summer of 1975, WS 10 was clearcut by high-lead logging techniques. Slash debris was removed from most of the channel and either piled above the high flow channel or moved to the top of the watershed by a cable carriage. Although there were some effects on the

channel, substrate characteristics were not greatly different than substrates prior to logging. The lack of canopy was the major change in WS 10 after logging.

Mack Creek is one of three major drainages within the H. J. Andrews Experimental Forest. Mack Creek is a third-order channel that drains a 650 ha watershed on the west slope of the Cascade Mountain Range. Headwaters originate at an altitude of 1400 m and the stream flows into Lookout Creek at 700 m. The stream gradient is 10% and the gradient of the side slopes is 77% (Froehlich 1973). The study section was a third-order stream with an average width of 3.8 m and an average depth of 0.1 m. Streamflows of 45 to 1000 l/sec were measured and higher flows occurred during storms. The streambed is composed of rocks of volcanic origin. The size distribution of substrates is heterogeneous, ranging from fine particles to boulders up to 2 m in diameter. The watershed receives approximately 225 to 250 cm of precipitation annually and most of that occurs from October through April. The precipitation is often in the form of snow from December through April, which results in a snowpack up to 1.5 m in depth.

A 3.5 ha section of Mack Creek had been clearcut in 1965 with high-lead logging techniques. After the area was logged, large debris was removed from the stream and then the clearcut was burned. The clearcut exposed approximately 350 m of channel. In 1975, young Douglas-fir and western hemlock were becoming established but no significant shading of the stream channel had occurred except for a small patch of willow at the lower end of the clearcut. Immediately above the clearcut section of Mack Creek was a 450 year-old Douglas-fir

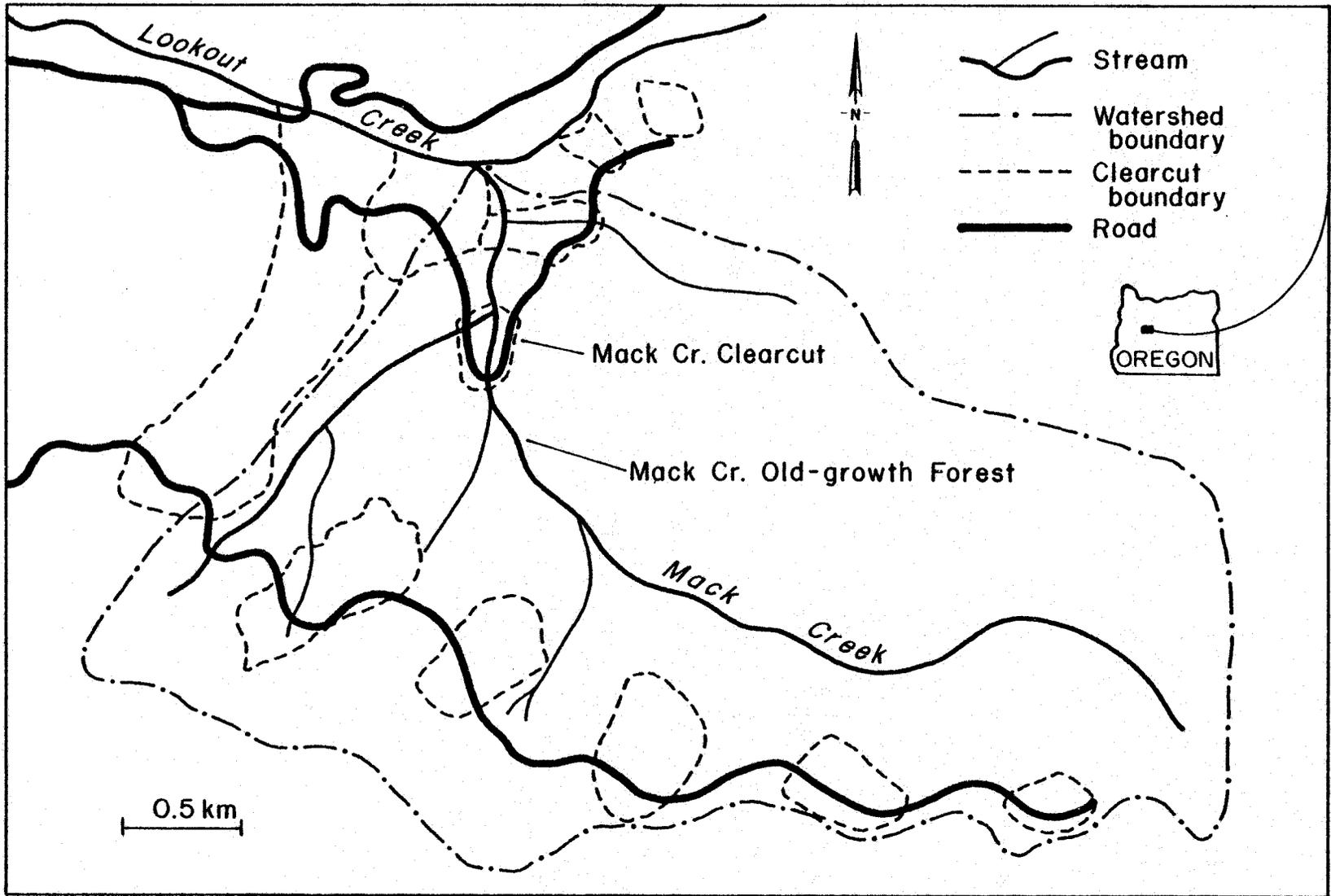
western hemlock forest (Fig. 1). The major difference between the two study sites, MC and MF, was the lack of canopy in the clearcut.

Lookout Creek is a fifth-order channel that drains the entire H. J. Andrews Experimental Forest, a 6000 ha watershed. Streamflows generally range from 200 l/sec in summer to over 30000 l/sec during winter storms. Stream gradient is approximately 3% and the streambed consists primarily of basaltic cobble and boulders. The stream is approximately 15 m wide; therefore, the canopy opening exposes most of the channel to direct solar radiation during most of the day. Also, Lookout Creek runs from east to west as opposed to Mack Creek, which runs from south to north; therefore, there is less topographic shading in Lookout Creek than in Mack Creek.

Grazer - Primary Producer Interaction

Laboratory stream channels at the Oak Creek Laboratory of Biology, Corvallis, Oregon, were used to examine the interaction of grazers and primary producers in flowing water. These artificial systems were employed because it was necessary to regulate density and type of grazers. Stream water in these channels was obtained from a tributary to Oak Creek. Water temperatures averaged 13°C during the study. Water was filtered through a sand and glass fiber filter to reduce the effects of colonization and introduction of other grazers. Light levels were artificially maintained by a bank of fluorescent and incandescent lights.

Fig. 1. Map of the Mack Creek drainage showing the relative positions of the forest and clearcut sites. Reduced map of Oregon on the right indicates the general location of the study area.



Old-growth - Clearcut Comparison

Primary production was compared in the old-growth and clearcut section of Mack Creek in the H. J. Andrews Experimental Forest, Lane County, Oregon. The study sites on Mack Creek, MF and MC, were described in the previous discussion of research locations in the studies of light-nutrient relationships. These paired sites on Mack Creek provided an excellent opportunity to compare the effects of shading on primary production. The small size of the clearcut minimized many of the cumulative downstream effects inherent in large-scale logging operations. There were practically no differences in temperature between the two sections; the greatest difference measured was 2°C. Sufficient time had elapsed (9 yrs) so that terrestrial vegetation was re-establishing and reducing sediment inputs to the stream. The channel gradient was steep enough that most of the past inputs of sediments had been flushed from the system. Nutrient concentrations in the clearcut section were not significantly higher than concentrations in the old-growth section. Therefore, the primary difference between the clearcut and old-growth sections was the amount of solar radiation reaching the streambed.

LIGHT-NUTRIENT RELATIONSHIPS WITH PRIMARY PRODUCTION

Many streams in the Pacific Northwest are heavily shaded and have very low concentrations of nutrients for primary production; therefore, primary production may be limited by either light or nutrients. I designed research to determine the degree to which primary production in streams was influenced by either light or nutrients and under what conditions the relative influence of these factors changed. I first examined diel patterns of nutrient concentrations in streams of the Cascade Mountains to determine the most probable nutrient that limited primary production. I then examined the response of primary producers in a small, heavily shaded stream to additions of light, a critical nutrient, and a combination of the two. The response was verified by repeating the experiment by shading a section of the stream after logging and observing primary production in shaded and open conditions, with and without addition of the critical nutrient.

Methods

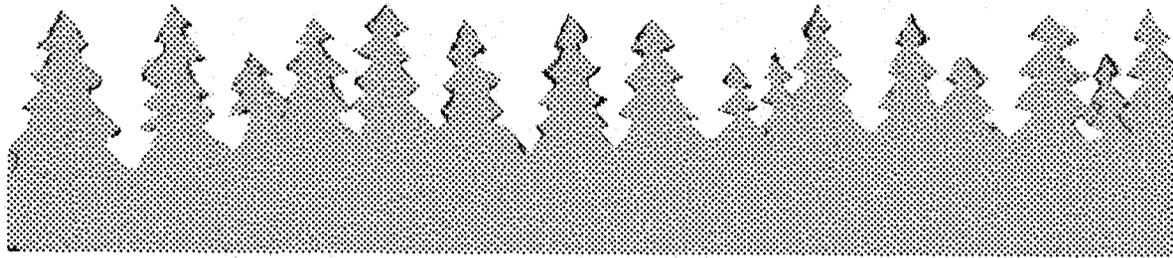
Diel patterns of nitrate and orthophosphate concentrations were measured at WS 10, MF, MC, and LO on 19 May 1974. Water samples were taken at 6-hr intervals, beginning at midnight and continuing through 6:00 PST at WS 10 and LO and through midnight at MF and MC. Water samples were taken in 300 ml BOD bottles that had been sequentially rinsed with 1.0 N HCl, 90% acetone, and distilled water. Samples were kept on ice immediately after collection and were filtered through Whatman GFC glass fiber filters within 36 hr of collection. These

samples were then stored at 3°C until analysis by the Central Chemistry Laboratory. Nitrate was determined by the cadmium reduction method (limit of detection - 0.7 µg/l) and orthophosphate was determined by the phosphomolybdate method (limit of detection - 1.0 µg/l).

Dissolved inorganic carbon was measured at the four sites on 9 September 1974. Duplicate water samples were taken at 3-hr intervals from sunrise to dawn of the following day and held on ice until analysis. Total dissolved inorganic carbon was determined by Gran titration (Talling 1973). All analyses were completed within 6 hr after collection.

Studies of the effects of light and nutrients were conducted on four sections of WS 10 when it was an old-growth forest. Four experimental treatments were established by placing artificial lights over the stream and adding NaNO_3 at the halfway point in the lighted section (Fig. 2). The artificial lighting was a combination of high intensity fluorescent, Gro-Lux fluorescent, and 150 W incandescent lights, all powered by a generator. A 12-hr photoperiod was simulated by a clock mechanism on the generator that automatically turned the generator on for 12 hours and off for 12 hours. The light level in the natural light section was 500 to 1000 lux and approximately 11000 lux in the sections with artificial light. Light measurements were made with a Weston foot-candle meter. Each of the two lighted sections was 2.5 m long. NaNO_3 was constantly added to the lower sections with a mariotte bottle. The nitrate solution in the bottle was adjusted every 2 days to compensate for changes in flow and to maintain a concentration of 100 µg $\text{NO}_3\text{-N}$ /liter in those sections. Nitrate concentrations in the

Fig. 2. Diagram of relative positions of treatment sections in the light and nitrate addition experiment in WS 10. Illumination and nitrate concentrations are indicated for each section.



ARTIFICIAL LIGHTS

OOOOOOOOOOOOOO

ADDITION OF NO₃



UPSTREAM

DOWNSTREAM

550-1100 lux
0-5 ppb NO₃

11000 lux
0-5 ppb NO₃

11000 lux
100 ppb NO₃

550-1100 lux
100 ppb NO₃

AMBIENT LIGHT

LIGHTED

LIGHTED

+ NO₃

AMBIENT LIGHT

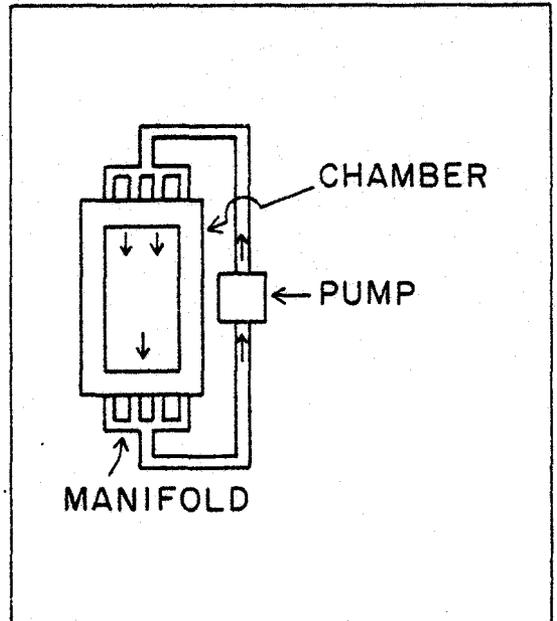
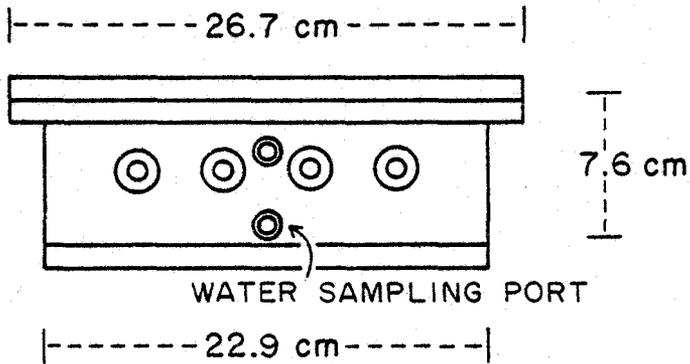
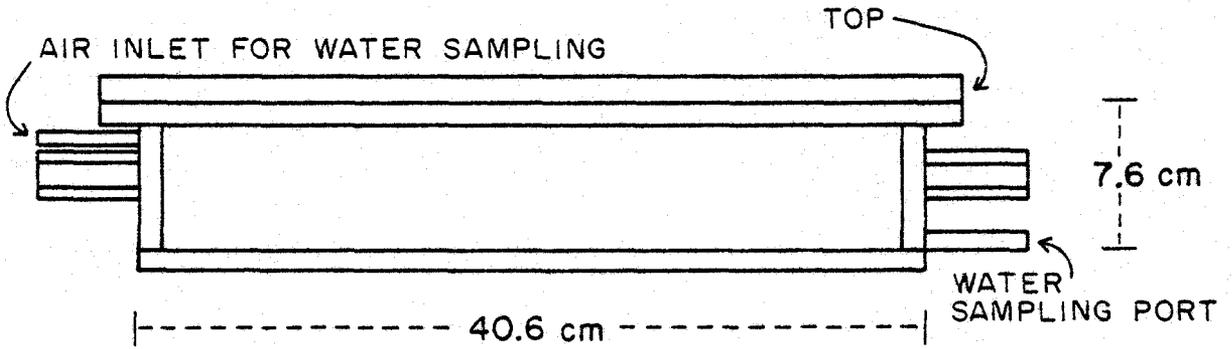
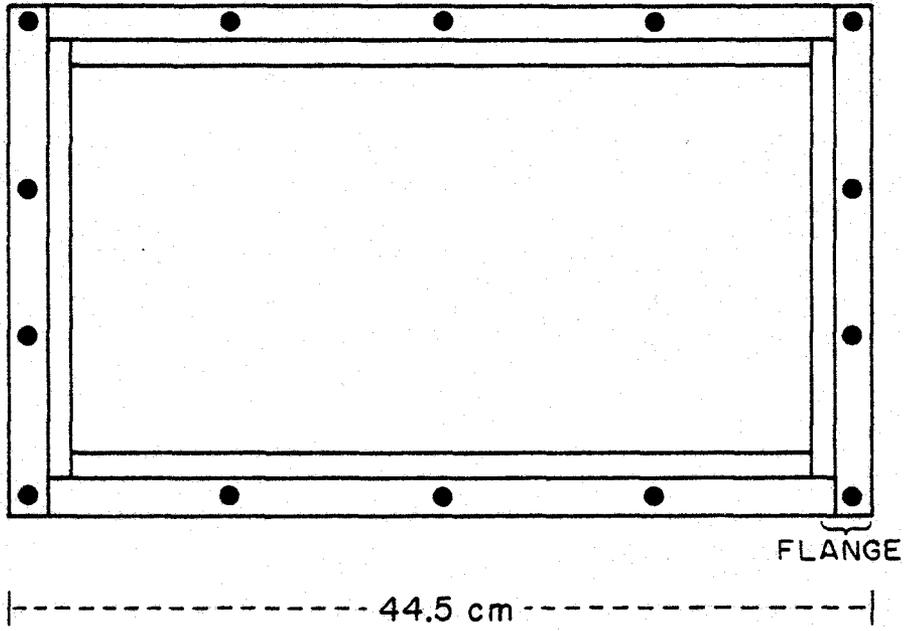
+ NO₃

unenriched sections were 0-5 $\mu\text{g NO}_3\text{-N/liter}$. Nitrate concentrations in larger local streams that supported substantial levels of primary production were approximately 50-100 $\mu\text{g NO}_3\text{-N/liter}$.

Smooth brick field tiles, 58.8 cm^2 , were placed in the four sections and used for chlorophyll a and primary production measurements. Five tiles were collected from each section at 7-day intervals throughout the 28-day study. Chlorophyll a was measured on these tiles by immersing the tile in 50 ml of 90% basic acetone for 24 hours in darkness at 4°C. Fifteen ml of the acetone solution were centrifuged for 5 minutes and decanted. Absorbance of the solution was read on a Beckman Model DB Spectrophotometer at 665 nm and 750 nm. After addition of 0.1 N HCl, absorbance was read again at 665 nm and 750 nm. The amount of chlorophyll a present was calculated by equations reported by Wetzel and Westlake (1969).

At the end of the study, benthic metabolism was measured on tiles in each section. Ten tiles were placed in a modified McIntire primary production chamber (Fig. 3). The chamber was closed and all air bubbles were eliminated from the chamber. Triplicate water samples were collected at the same time with special care to exclude air bubbles; 125 ml wide mouth, polypropylene bottles were rinsed three times and capped under water. Total inorganic carbon was determined on these samples within three hours by measuring initial pH and total alkalinity. Alkalinity was determined by Gran titration of the sample with 0.10 N HCl within a pH range of 3.8 to 4.5 (Talling 1973). Total inorganic carbon was estimated from initial pH and total alkalinity (Stumm and Morgan 1973). This technique required a very precise,

Fig. 3. Diagram of chamber used for measurement of periphyton metabolism. Arrangement of the chamber, manifold, and pump during operation is illustrated in the inset.



battery-operated pH meter. A Coleman 37A pH meter was selected for this research because it was a null balance meter that operated continuously over the full pH scale and had an accuracy of ± 0.005 pH units and a precision of ± 0.001 pH units. Net community primary production was measured in the chamber during daylight and community respiration was measured during darkness; gross primary production was calculated from these two measurements. Duplicate estimates of periphyton metabolism were made for each section.

At the end of the closure period, water samples were withdrawn from the chamber to determine the inorganic carbon concentration after incubation. Triplicate water samples were drawn from the sampling port in the bottom of the chamber and introduced into sample bottles by a rubber tube that directly connected the chamber to the bottle. Sample bottles were constructed so that water filled from the bottom and overflowed out a release port in the top, thereby minimizing atmospheric mixing with the sample. A volume of water equivalent to three times the volume of the bottle was allowed to pass through before the sample bottles were clamped off. Total inorganic carbon was determined on these samples as previously described. After the samples were taken, the chamber was flushed for 5 minutes with fresh stream water and closed again to begin another sampling interval. After completion of all measurements for a set of substrates, the tiles were removed and chlorophyll a was measured as previously described.

Measurement of changes in dissolved gases provides estimates of benthic metabolism; not every method measures the same process nor has the same constraints. Each of the available methods for measurement

of primary production gives estimates of specific types of metabolic rates. Metabolism measured during daylight represents net community primary production (NCP), which is gross primary production (GPP) minus autotrophic respiration (AR) and heterotrophic respiration (HR):

$$\text{NCP} = \text{GPP} - \text{AR} - \text{HR}.$$

Net community primary production must not be confused with net primary production, which is gross primary production minus autotrophic respiration alone. It must also not be confused with net community production because heterotrophic production derived from allochthonous dissolved organic matter is included in net community production but not in net community primary production. Metabolism measured during the night represents community respiration (CR), which is autotrophic respiration plus heterotrophic respiration:

$$\text{CR} = \text{AR} + \text{HR}.$$

Gross primary production is estimated by adding community respiration for daylight hours to net community primary production:

$$\text{GPP} = \text{NCP} + \text{CR}_{\text{daylight}}$$

Community respiration at night is assumed to be the same as community respiration during the day. Community respiration was measured during night to avoid disruption of the metabolic rhythm of the periphyton. Beyers (1963) found evidence suggesting a rhythm, but in White Clay Creek estimates of respiration in daylight or night were both found to be equal (Bott et al. 1978).

Structure of the diatom community in each section was determined from glass slides that were incubated throughout the study. Glass slides were placed in each section and two slides were collected at

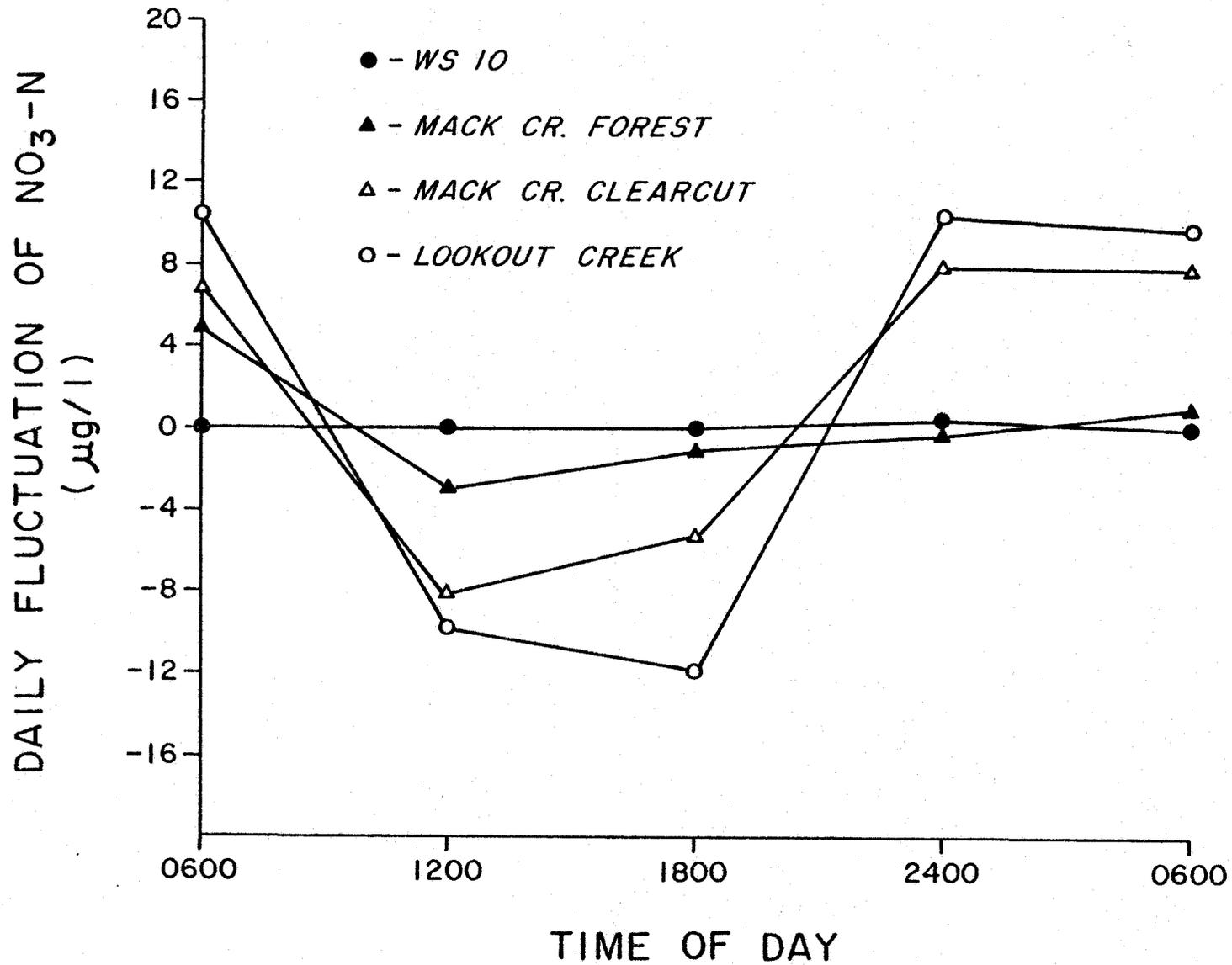
7-day intervals. Cell density and community structure measurements were based on direct counts of diatom cells in an area of 1.2 cm² on the slide. Community structure of the diatom community was analyzed by Dr. David Busch (Dept. of Botany and Plant Pathology, Oregon State University).

Watershed 10 was clearcut in the summer of 1975; the clearcut watershed provided an opportunity to check the study of the effects of light and nitrate by artificially shading a section of stream. Because nutrient response of the watershed was being closely monitored, no continuous addition of nutrients was possible. A 5 m section of stream was covered with a shade screen that transmitted 8% of incident solar radiation. Natural substrates were placed in wire baskets and allowed to colonize for 8 weeks. Three baskets of substrates were collected for chlorophyll a analysis and two were used for primary production. Primary production and community respiration were measured as previously described. Nitrate was added to one of the chambers in both the shaded and unshaded sections to raise the concentration in the chamber to 100 µg NO₃-N/liter.

Results

Metabolic activity by aquatic biota caused diel patterns of nutrient concentrations in these streams. Nitrate displayed diel patterns in three of the four streams sampled in this study (Fig. 4). Maximum change in nitrate occurred during daylight and the greatest decrease in concentration was found in the most open site. Relative change in nitrate concentrations decreased as the sites became more shaded. The pattern of change relative to shading and the decrease occurring

Fig. 4. Diel changes in nitrate concentrations in four streams in the H. J. Andrews Experimental Forest on 19 May 1974 (expressed as fluctuation around mean daily concentration of $\text{NO}_3\text{-N}$ in $\mu\text{g/l}$).



during daylight suggest that aquatic primary production may have caused the diel pattern of nitrate concentration. Orthophosphate showed no diel patterns in any of the sites. The apparent uptake of nitrate and lack of uptake of orthophosphate suggest that the demand for nitrate was a major portion of the supply of nitrate but that sufficient phosphorus was available to satisfy demand.

If the diel pattern of nitrate concentrations were caused by uptake by primary producers, a similar pattern might also be observed in dissolved inorganic carbon. Such a response was observed in the four streams, with the greatest change occurring at the most open site and the least change in the most shaded site (Fig. 5). Therefore, the observed patterns of nitrate and dissolved inorganic carbon suggest that primary producers in streams can significantly alter nutrient concentrations.

Accumulation of algae on artificial substrates in WS 10 was influenced by increased light, but additional nitrate had no effect without additional light (Fig. 6). Colonization of algae was not significantly different between the natural light section and the natural light section that received nitrate addition (Student's *t* test, $p < 0.05$). However, the standing crop of chlorophyll a that developed in the lighted section was significantly greater than that in either of the unlighted sections; the standing crop of chlorophyll a in the lighted section that received nitrate addition was significantly greater than that in the lighted section without added nitrate. Standing crop of chlorophyll a in the lighted section was 5 times greater than in the unlighted sections. Chlorophyll a concentrations in the lighted

Fig. 5. Diel changes in concentrations of inorganic carbon in four streams in the H. J. Andrews Experimental Forest on 9 September 1974 (expressed as fluctuation around mean daily concentration of inorganic carbon in $\mu\text{M}/\text{l}$).

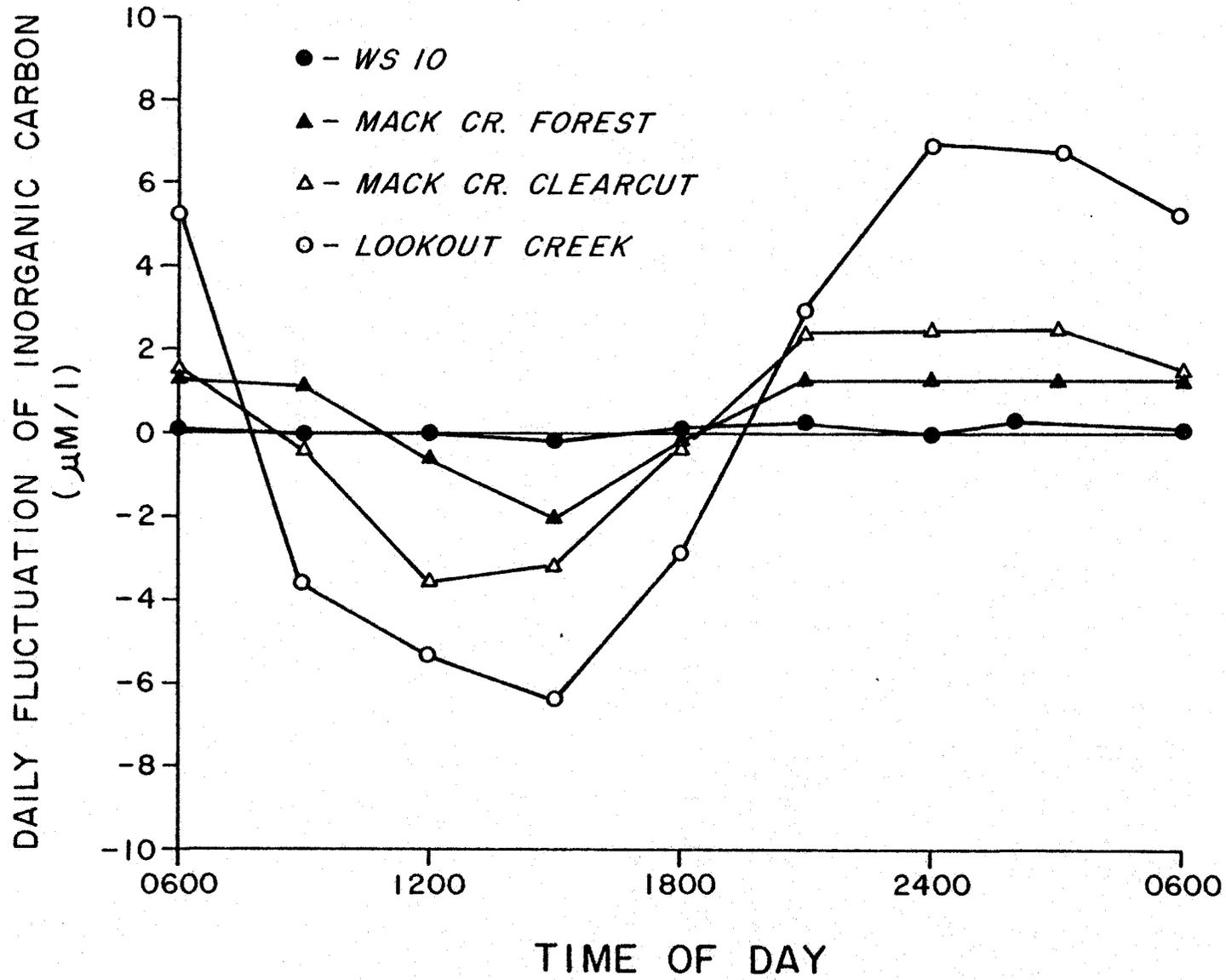
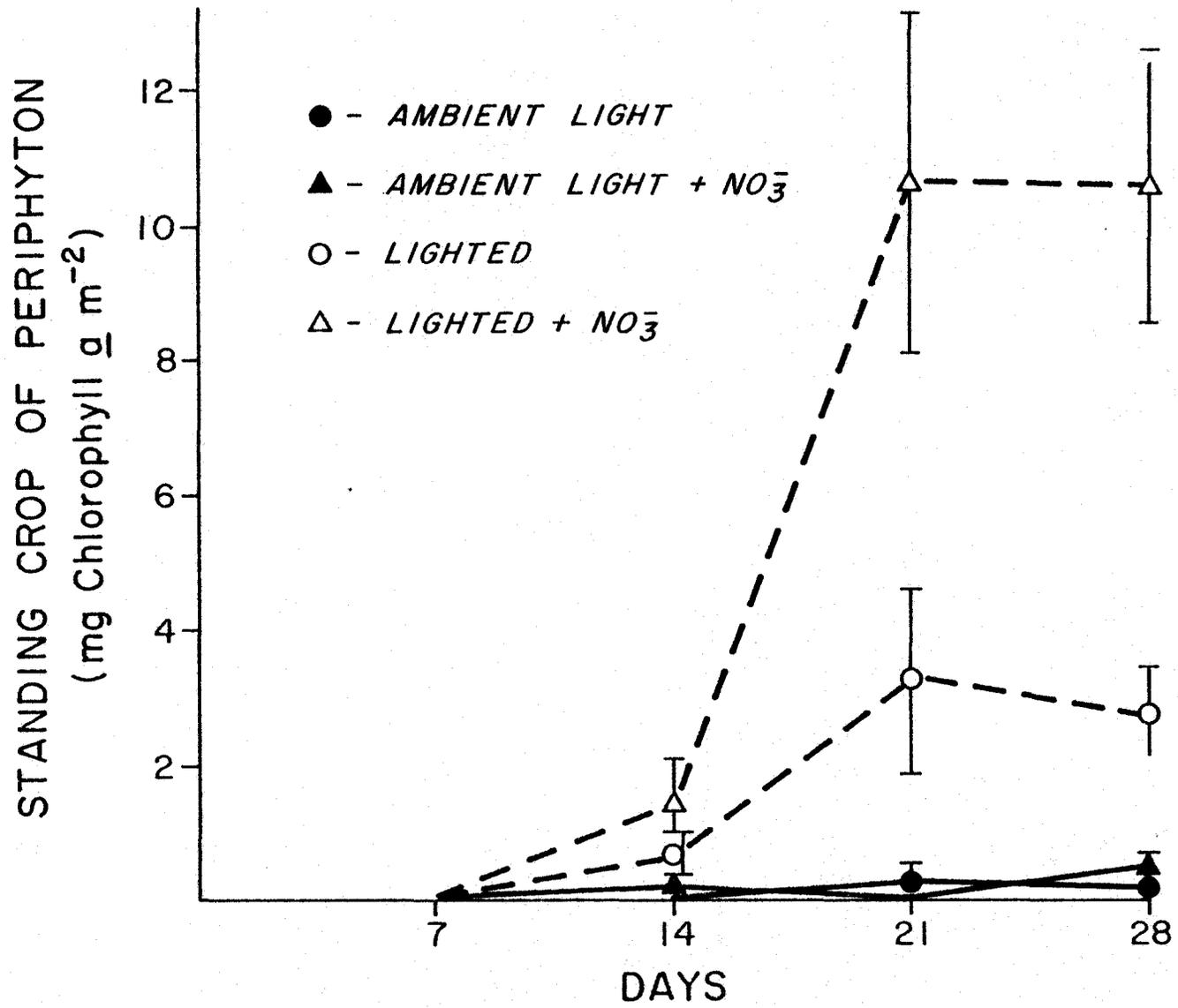


Fig. 6. Standing crops of chlorophyll a in the sections with ambient light, ambient light with addition of nitrate, lighted, and lighted with addition of nitrate in WS 10 during a 28-day study in August 1974. Points represent means of five samples and bars indicate one standard deviation.



section that received nitrate addition were 20 times greater than those in the unlighted sections and 3.5 times greater than those in the lighted section.

Rates of gross primary production and community respiration at the end of the study period displayed a similar pattern to that of algal colonization (Fig. 7). No difference in primary production was detected between the natural light and natural light section that received nitrate addition (Student's *t* test, $p < 0.05$). The rate of gross primary production was elevated in the lighted sections, reaching a maximum in the lighted section that received nitrate addition. The relative response of respiration for the sections was similar to the relative response of gross primary production.

Only in the lighted sections did gross primary production even begin to balance metabolic losses through community respiration as evidenced by P/R ratios (gross primary production/community respiration for a 24-hour period) greater than 1.0 (Fig. 8). Primary production more than compensated for community respiration on substrates in the lighted section that received nitrate addition. However, gross primary production was far less than respiratory demand in the natural light or natural light section that received nitrate addition. This does not mean that the algae were not able to meet their own respiratory demands, but rather that they were not able to supply all the energy needed to support the epilithic communities of algae, bacteria, and fungi. In the lighted sections, however, the autotrophs were able to produce enough organic matter to support the respiration of the epilithic communities. These results suggest that light is the most critical factor affecting

Fig. 7. Rates of gross primary production and community respiration in the unlighted, lighted, lighted with nitrate addition, unlighted with nitrate addition sections in WS 10 at the end of a 28 day study in August 1974. Each histogram represents the mean of two determinations and bars indicate range.

BENTHIC METABOLISM
(mg C m⁻² day⁻¹)

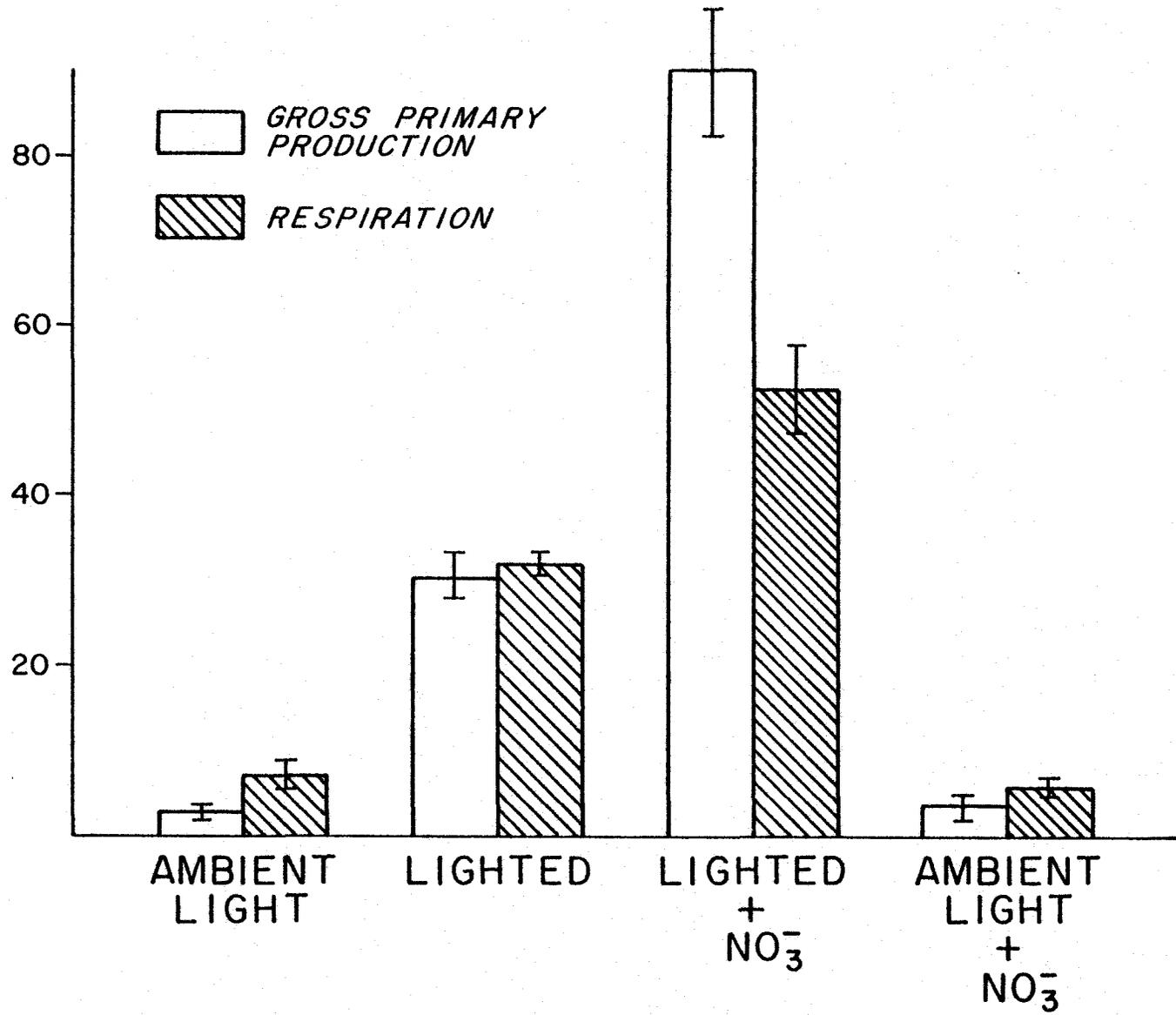
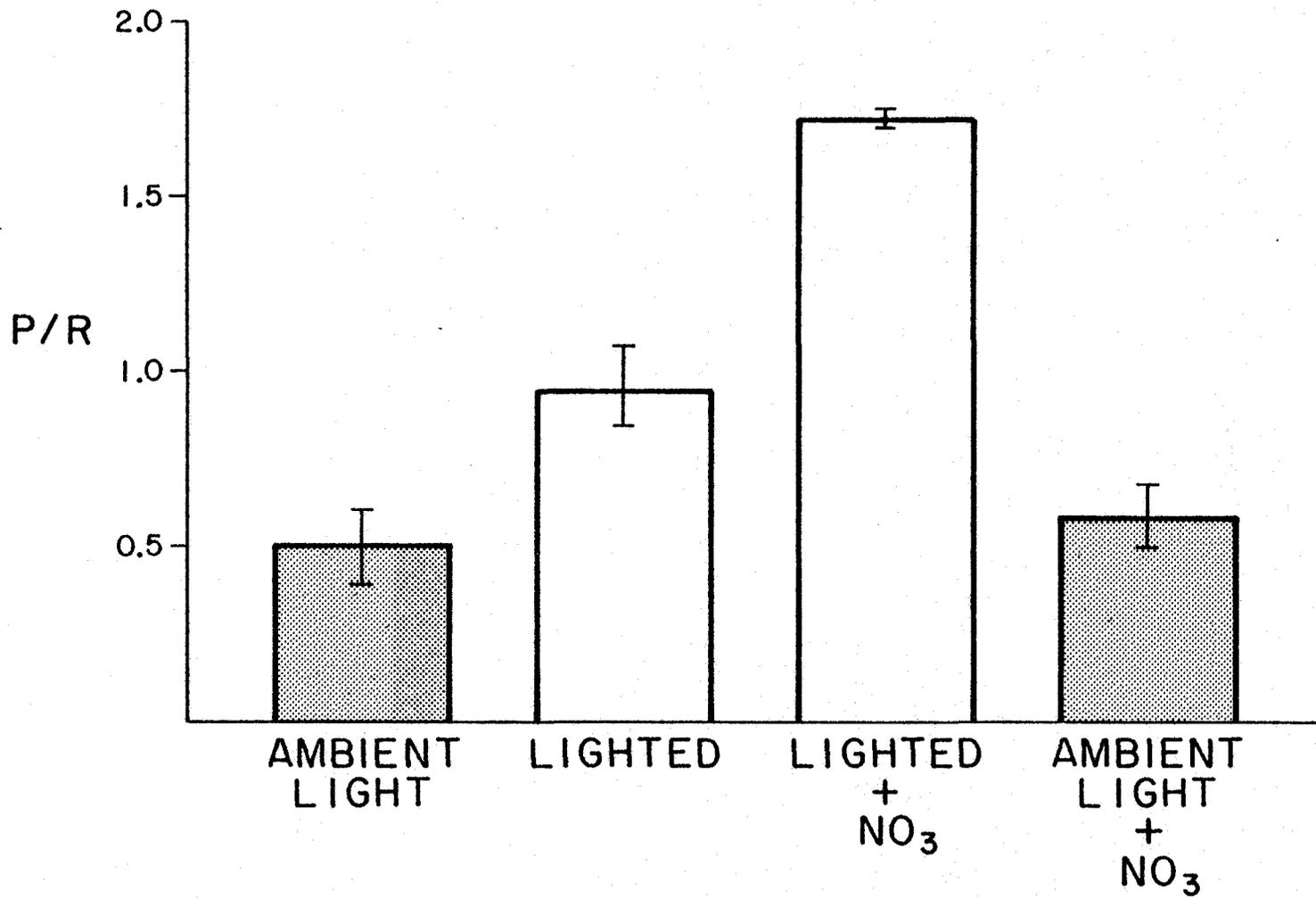


Fig. 8. P/R ratios in the unlighted, lighted, lighted with nitrate addition, and unlighted with nitrate addition sections in WS 10 at the end of a 28 day study in August 1974. Each histogram represents the mean of two determinations and bars indicate range.



primary production in forested streams and additional nutrients become significant only after there is sufficient light.

Relative abundances of diatom species also changed in response to addition of light (Table 1). Achnanthes lanceolata, Cocconeis placentula var. lineata, Eunotia pectinalis, and Meridion circulare showed the greatest response to increased light. Achnanthes lanceolata was the most prolific taxon on most of the slides and this diatom is commonly observed early in algal colonization in streams (McIntire 1966). In the lighted sections, Achnanthes lanceolata composed more than 90% of the diatom assemblage. The four species that showed a response to light were found in small concentrations in the natural light sections, particularly Meridion circulare. Diatoma heimale var. mesodon, Gomphonema intricatum var. pumila, G. parvulum, G. subclavatum, and Navicula radiosa var. tenella were the most abundant of those taxa showing little response to increased light intensity. Community structure of diatoms in the lighted section was relatively similar to the community structure in the lighted section that received added nitrate. Therefore, there appeared to be no response of community structure to additional nutrient under lighted conditions.

Results of the light and nitrate addition experiments were verified in the same watershed two years later. In the interim, the watershed had been clearcut and most of the riparian vegetation had been removed. A section of stream was artificially shaded with a screen that blocked 92% of incoming solar radiation. Standing crop of chlorophyll a on tiles in the shaded section was 1.41 ± 0.32 mg chlorophyll a m^{-2} ($\bar{x} \pm 1$ SD) and in the open section it was 4.94 ± 0.73 mg chlorophyll a m^{-2} .

Table 1. Densities and relative abundances of diatom taxa on glass slides in the natural light, lighted, lighted with nitrate addition, and natural light with nitrate addition sections in WS 10 in August 1974. Cell numbers per cm² are reported in the columns and relative abundances are indicated in the parentheses.

Treatment Sections	A. lanceolata	C. placentula	Taxa			Total	
			D. hiemale var. mesodon	G. intricatum var. pumila	G. parvulum		G. subclavatum
Natural Light							
Without NO ₃							
21 days	138(44)	28(9)		68(22)		79(25)	312(100)
28 days	149(18)	46(6)		559(67)		80(10)	834(100)
With NO ₃							
21 days	85(54)	22(14)		34(22)		15(10)	157(100)
28 days	104(29)	21(6)		195(55)		36(10)	356(100)
Lighted							
Without NO ₃							
21 days	153(41)	38(10)		164(43)		23(6)	378(100)
28 days	32624(91)	1226(3)		1247(4)		576(2)	35673(100)
With NO ₃							
21 days	1935(48)	408(10)		1448(36)		287(7)	4078(100)
28 days	134449(95)	4882(4)		365(0.3)		200(0.1)	139896(100)

Standing crops of primary producers for both sections were slightly greater than those in the natural light and lighted sections of the initial experiment, but the relationships between the sections remained the same. The difference between the experiments was most likely a result of longer photoperiods (12 hr in the original experiment and 14 hr in the later study), higher light levels (1100 lux and 11000 lux in the original experiment as compared to 1650 lux and 110000 lux in the later study), and longer incubation time (4 weeks in the original study and 8 weeks in the later study). Nonetheless, there was a significant increase in the standing crop in the open section (Student's t test, $p < 0.05$).

Rates of gross primary production were also greater in the open section than in the shaded section (Fig. 9). After substrates were incubated at $100 \mu\text{g NO}_3\text{-N l}^{-1}$ for 24 hours, gross primary production was greater in the open site than in the open section without addition of nitrate. In the shaded section, P/R ratios were substantially less than 1.0, both with and without nitrate addition (Fig. 10). In the open section, P/R ratios were also less than 1.0 but approached unity; however, gross primary production was well in excess of respiratory demand. In general, similar responses of primary production to experimental manipulation of light and nitrate levels were observed under both an old-growth forest condition and an open clearcut situation.

Discussion

Nitrogen was the most probable nutrient that potentially limited primary production in streams of the H. J. Andrews Experimental Forest

Fig. 9. Rates of gross primary production and community respiration in the open and shaded sections of WS 10 one year after clearcutting. Response to nitrate addition was examined by addition of nitrate in the chambers for 24 hours prior to measurement. Each histogram represents the mean of two determinations and bars indicate range.

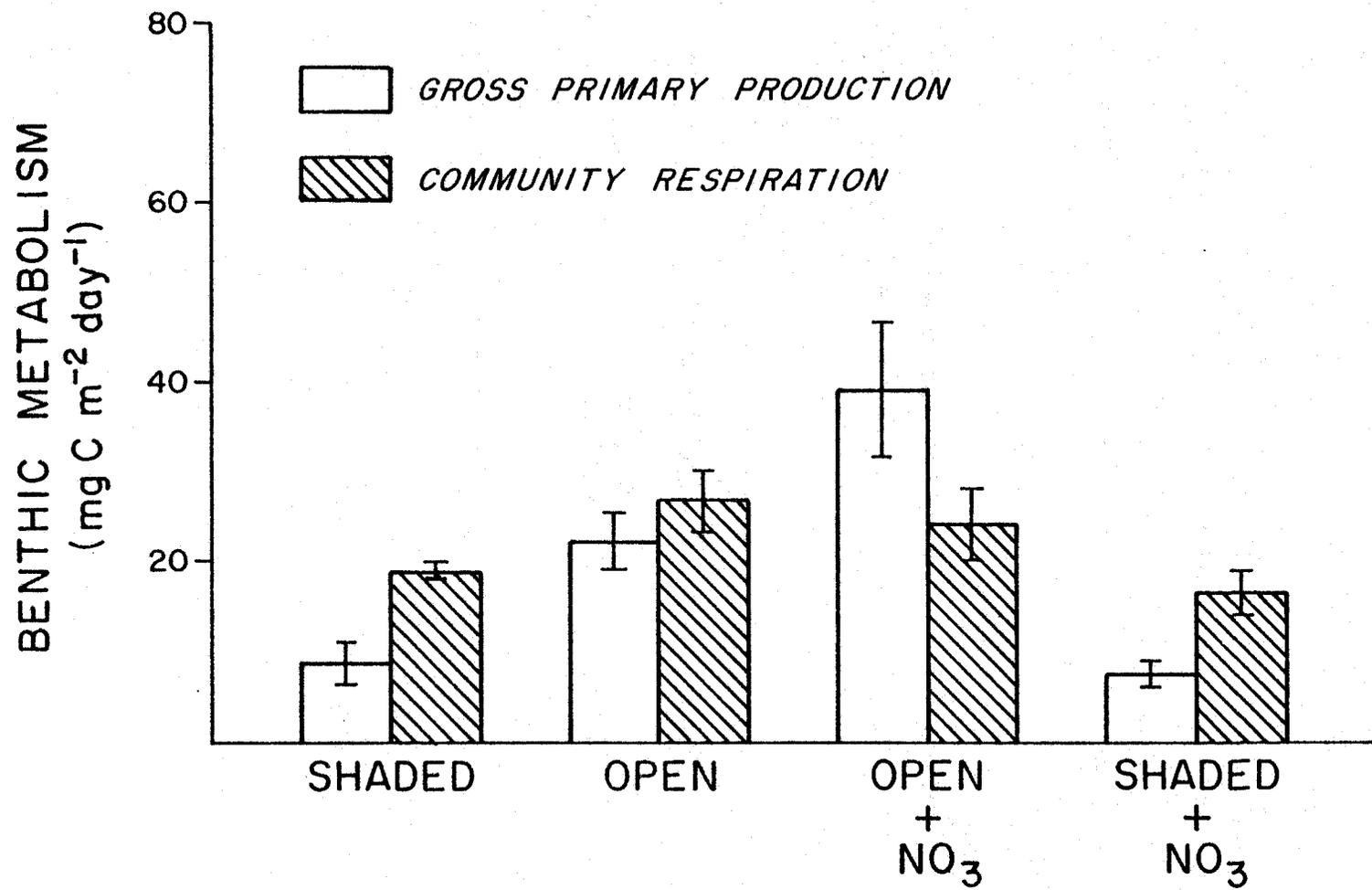
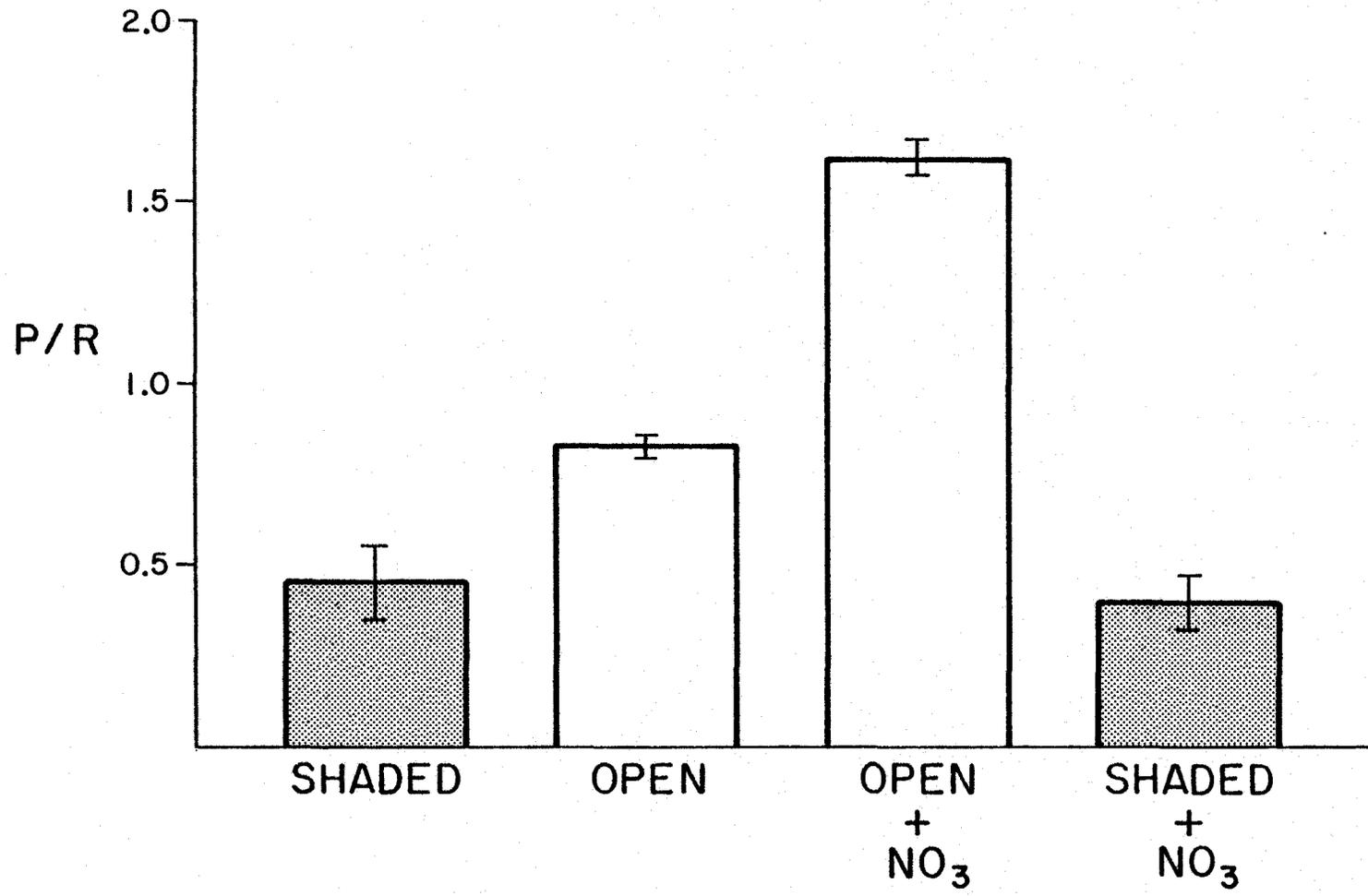


Fig. 10. P/R ratios in the open and shaded sections, with and without addition of nitrate, in WS 10 one year after clearcutting. Each histogram represents the mean of two determinations and bars indicate range.



during this study. Ratios of nitrogen to phosphorus in stream water, diel patterns of nutrient concentrations, and response of the primary producers in the light and nitrate addition experiment provided evidence that nitrogen was more critical than phosphorus in regulating rates of primary production.

Ratios of inorganic nitrogen to orthophosphate (N/P) provided an initial indication that primary producers would be nitrogen limited in the streams of the H. J. Andrews Experimental Forest. During my study, N/P ratios were observed ranging from 0.2 to 2.0. Redfield (1958) suggested that aquatic primary producers would be nitrogen limited at atomic ratios of N/P less than 15 and phosphorus limited at ratios greater than 15, because cellular N/P ratios are approximately 15. This concept was empirically tested in recent studies and the critical ratio was found to be 30 (Rhee 1978). N/P ratios in my study fell well within nitrogen limited conditions as defined by these authors. Approximately half of the surface waters in the state of Washington were designated nitrogen limited in a study by Thut and Haydu (1971) that used a very conservative N/P ratio of 10 as an index. They found that streams that were nitrogen limited most often originate in volcanic formations and phosphorus limited streams most often drain glacial or granitic geological formations.

Diel patterns of nitrate and orthophosphate in four streams showed that nitrate was taken up appreciably in the unshaded streams; however, phosphorus was only slightly removed. Primary producers in the streams were most likely responsible for the uptake. The lack of nitrate uptake at night or in the heavily shaded stream indicated that primary producers

were responsible for the change and that light intensity influenced nutrient utilization. Activity of nitrate reductase, the enzyme necessary for utilization of nitrate in plants, is induced by light (Schwoerbel and Tillmanns 1971, Packard 1973). Changes in inorganic carbon in my study streams also indicated that primary producers could have caused the patterns of uptake. Reduction of nitrate concentrations showed that demand for nitrate by primary producers exceeded the supply but the lack of change of orthophosphate indicated that phosphorus was in sufficient supply. Therefore, of the two major nutrients, nitrogen and phosphorus, nitrogen would most likely be limiting to primary production because of the deficit between its supply and demand.

Alteration of nutrient concentrations in lotic ecosystems by primary producers has been observed in other studies and used as an indicator of nutrient limitation. Nitrate concentration decreased downstream in the Silver Springs system but orthophosphate concentrations decreased only slightly (Odum 1957). The N/P atomic ratio in Silver Springs was 8.05, which would indicate nitrogen limitation according to Redfield (1958) or Khee (1978). Odum concluded that nitrogen was more likely to be limiting to primary production than phosphorus. McColl (1974) found that both ammonia and nitrate decreased downstream in a stream in New Zealand; no decrease was observed in a stream below a sewage outfall that introduced high concentrations of nitrogen and phosphorus. Periphyton in laboratory streams was able to rapidly remove nitrate and ammonia from the water (Ehrlich and Slack 1969). A number of studies have demonstrated with radioactive phosphorus that primary producers in streams can actively remove phosphorus and substantially

alter stream chemistry (Odum and Hoskin 1959, Ball and Hooper 1963, Whitford and Schumacher 1964, Nelson et al. 1969, Sperling and Grunewald 1970, Gregory 1978). Uptake of stable orthophosphate was observed in a New Zealand stream (McColl 1974). Diatoms in streams have been shown to cause reductions in silica (Swale 1969, Wang and Evans 1970, Lack 1971, Edwards 1973). Therefore, my study and others have demonstrated that primary producers in lotic systems can alter concentrations of nutrients in stream water if metabolic demand is great relative to supply.

Many land-use practices result in increased nutrient runoff into streams and, therefore, may enhance aquatic primary production. Nitrate concentrations in streams that drain logged watersheds increase as much as 3 to 40-fold as compared to undisturbed conditions (Fredriksen 1970, Likens et al. 1970). Elevated nutrient concentrations gradually decrease as watersheds revegetate; therefore, the potential for nutrient stimulation of primary production is greatest in the first few years after clearcutting. Forest fertilization in the Pacific Northwest also contributes additional loads of inorganic nitrogen to streams (Thut and Haydu 1971, Fredriksen, Moore, and Norris 1975). Elevation of nitrogen concentrations in streams as a result of fertilization generally lasts only for a few months. However, fertilization of low gradient, deep soil watersheds may result in increased nitrogen concentrations in streams for several years (personal communication, Dr. J. R. Sedell, U.S. Forest Service). Therefore, land-use practices in the Northwest may potentially increase concentrations of nitrogen in streams and, thereby, stimulate aquatic primary producers.

Previous studies have demonstrated that nutrients may stimulate primary production in streams. Nitrogen was added continuously and intermittently to artificial channels for 2 years and compared to an untreated channel in Kalama Springs, Washington (Speir 1979). Primary production was stimulated for the first 6 months. After that time primary production was equal in all streams; however, biomass of periphyton remained elevated in the channel that received continuous addition of nitrate. Grazers were considered responsible for the equalization of production after 6 months. Addition of nitrate to a laboratory stream resulted in increased rates of gross primary production (Sumner 1980). Several studies have shown that phosphorus could limit primary production in lotic systems (Traeen 1975, Wuhrmann and Eichenberger 1975, Fraleigh 1978, Stockner and Shortreed 1978). Other researchers have found that inorganic carbon can limit primary production in streams (McIntire and Phinney 1965, Wiegert and Fraleigh 1972, Boylen and Brock 1973, Dickman 1973). The mechanism for carbon limitation is poorly understood and may be more complex than a simple nutrient limitation because inorganic carbon is the major regulator of pH and buffering capacity in most streams. Nutrients are simply elements that are required for tissue elaboration and nutrient limitation is determined by metabolic demand, form of the element, and supply.

Light is one of the basic requirements for photosynthesis; therefore, light conditions must also be considered in questions of nutrient limitation. The study of light and nitrate addition in WS 10 demonstrated that nitrate potentially limited primary production but that it was limiting only after there was sufficient light. Limitation of primary

production could be viewed as a sequential process; first, light intensity is limiting, but after photosynthesis is light saturated, nutrients become limiting. This general pattern of response of primary producers to light and a limiting nutrient was supported in the experiments in the heavily shaded stream and the same stream after it was exposed to full sunlight by logging.

Other studies have also observed light limitation of primary production at low light levels and nutrient limitation at high light levels. Primary production in a laboratory stream was not influenced by concentrations of inorganic carbon at illuminations less than 7370 lux, but when light exceeded 11000 lux, rates of primary production increased with increasing concentrations of carbon dioxide (McIntire and Phinney 1965). Increases in light beyond 11000 lux had no effect on primary production at a given nutrient concentration. Light levels in the lighted section of the experiment in WS 10 were approximately 11000 lux, similar to the light saturation point found by McIntire and Phinney. In artificial channels at Kalama Springs, Washington, a research facility of the Weyerhaeuser Company, nitrate was added to open and shaded sections (Busch 1978). Nitrate had no effect on primary production in the shaded channels; however, both standing crops of primary producers and rates of primary production were greater in the open channel than in the shaded channel. Greatest rates of primary production and highest standing crops were observed in the open channel that received addition of nitrate. In Carnation Creek on Vancouver Island, British Columbia, researchers added nitrate and orthophosphate in troughs and observed accumulation of algae as

an index of primary production (Stockner and Shortreed 1978). Algal growth during the first 57 days was enhanced by addition of phosphorus and was greatest when concentrations of both nitrate and orthophosphate were tripled. During the second half of the experiment, light intensities dropped and nutrients had no effect on algal accumulation. Stockner and Shortreed concluded that algal growth during the second phase of their experiment was light limited and, therefore, nutrients had no effect. In laboratory streams at Oregon State University, primary production was greater in a lighted channel than in a shaded channel; in a lighted channel that received additions of nitrate, primary production was greater than either the lighted or shaded channels (Sumner 1980). Agreement among these studies of primary producer responses to light and nutrients in streams and the response I observed in the old-growth forested stream, WS 10, strongly supports the concept that light is the initial regulator of primary production in shaded streams and that nutrient limitation comes into play only after primary producers are light saturated.

EFFECTS OF GRAZERS ON PRIMARY PRODUCERS

Primary producers in streams are regulated by environmental factors that influence rates of production but may also be controlled by consumers. Responses of primary producers in streams to changes in environmental factors may be obscured by differential rates of grazing. Studies even have demonstrated that primary production in aquatic systems may be enhanced at intermediate grazing rates. I designed this research to determine the response of primary producers to different rates of grazing. The experiment was coordinated with other researchers to examine responses of the grazers and community structure of the algae.

Methods

Effects of grazers on primary production in flowing water were investigated in laboratory streams at the Oak Creek Laboratory of Biology in Corvallis, Oregon. Five identical stream channels were lined with smooth, brick field tiles along the bottom. The channels were 3 m long, 9.5 cm wide, and water depth was 3.2 cm; water velocity in the channels was 8.1 cm sec⁻¹. Water was recirculated and the replacement rate was 0.75 l/min. A bank of fluorescent lamps and incandescent flood lights provided a light intensity of 2300-3000 lux.

An aquatic snail, Juga silicula, which is common in streams of the Pacific Northwest, was selected as a representative grazer in this study. Juga is a rasping grazer but can be a generalist feeder as well. A slurry of algae scraped from substrates in Oak Creek was introduced

into each channel 2 weeks prior to stocking of grazers. Snails were stocked in the channels at densities of 0, 85, 170, 510, and 1020 snails m^{-2} . All snails were between 8 and 11 mm in length and weighed approximately 13 mg; therefore, standing crops of snails in the channels were 0, 1.11, 2.22, 6.66, and 13.26 $g m^{-2}$. Estimates of standing crops of snails in Oak Creek, a forested valley stream, at this time ranged from 4.5 to 20 $g m^{-2}$ (personal communication, Dale McCullough, Oregon State University). Glass slides were placed on edge between tiles to create turbulence in the channel; without this turbulence the snails tended to climb the sides of the channels. Snails tended to clump at the ends of the sections so they were redistributed every other day to prevent localized effects.

Three tiles were removed every 5 days for determination of standing crop of chlorophyll a by the methods already discussed. One tile was removed at the same time for determination of ratios of biomass/chlorophyll a. Periphyton was scraped from the tile and slurried in water. Half the sample was filtered, dried in the oven at 50°C, ashed in a muffle furnace at 500°C for 4 hours, and reweighed. Ash-free dry weight was estimated by subtracting the ash weight (minus filter ash) from oven dry weight. The other half of the sample was filtered and placed in a 90% solution of basic acetone in darkness for 24 hours. The acetone solution was then centrifuged for 5 minutes and decanted. Chlorophyll a concentration was calculated as previously described. The biomass/chlorophyll a ratio was computed by dividing the ash-free dry weight by the chlorophyll a concentration. Chlorophyll a standing crops for each day were converted to biomass of periphyton by the

biomass/chlorophyll a ratio (B/C) determined for each channel for each date (grazing reduced standing crops of periphyton at the heavy and intermediate densities of snails to the point that B/C ratios could not be determined at each sampling date; B/C ratios at the start and end of the experiment were extrapolated throughout the study).

Gross primary production, net community primary production, and community respiration were measured on two tiles in small chambers specifically designed for the tiles. Periphyton metabolism was measured for each channel at day 0, 15, and 35. Duplicate measurements were made for each channel on each date; measurements were made in a water bath with a light bank adjusted to match the light intensity over the laboratory channels. Techniques for estimation of metabolic rates were identical to those described in detail in the previous chapter. Chlorophyll a concentrations on the sets of tiles were determined to estimate the production per unit weight of periphyton in each channel. At the end of the experiment, rates of gross primary production were determined at different light levels for substrates from the control channel and the channel with high density of snails. The relationship between primary production and light for each of the channels was examined to determine change in photosynthetic response.

Snail growth rates and grazing rates were determined for each channel at the start and end of the study by Dale McCullough (Dept. of Fisheries and Wildlife, Oregon State University). Growth rates were determined by repeated weighings of 20 individually marked snails in each channel. Grazing rates and assimilation rates were measured by a dual isotope technique with ^{14}C and ^{51}Cr (Calow and Fletcher 1972).

Therefore, grazing pressure in each of the channels could be calculated from the ingestion rate per unit weight of snail and the standing crop of snails.

Change in taxonomic structure of primary producers was studied by Dr. David Busch. One tile was sampled every 5 days for analysis of taxonomic structure. Algae were scraped from the tiles, preserved, and counted with an inverted microscope.

Results

Standing crops of primary producers were impacted by grazing at the highest grazer density (snail density of 13.3 g m^{-2} or SD_{13}) and the intermediate grazer density (snail density of 6.7 g m^{-2} or SD_7) (Fig. 11). Standing crop of chlorophyll a continually increased throughout the 35-day study at both of the low densities of grazers (snail density of 2.2 g m^{-2} or SD_2 ; snail density of 1.1 g m^{-2} or SD_1) and the control (no snails or SD_0). Rates of increase of standing crop of chlorophyll a at SD_0 , SD_1 , and SD_2 were not significantly different; however, the rate of increase at SD_7 was significantly lower. The rate of decrease at SD_{13} was significantly different than any of the channels (Table 2). Final standing crops of chlorophyll a at SD_0 , SD_1 , and SD_2 were 3.7 times higher than those at SD_7 and 26.2 times higher than those at SD_{13} . Thus, grazer density at or greater than 6.66 g m^{-2} was sufficient to reduce the accrual of primary producers.

Grazers affected the physiological state of the primary producers. As communities of primary producers at SD_0 , SD_1 , and SD_2 developed, biomass/chlorophyll a ratios (B/C) increased approximately 60% (Fig. 12).

Fig. 11. Standing crops of chlorophyll a through time under different grazing pressures. Points represent means of samples for sampling dates.

$$(Y_{SD_0} = 35.54e^{0.045x}, Y_{SD_1} = 37.28e^{0.045x}, Y_{SD_2} = 29.06e^{0.051x}, \\ Y_{SD_7} = 34.61e^{0.011x}, Y_{SD_{13}} = 23.88e^{-0.040x})$$

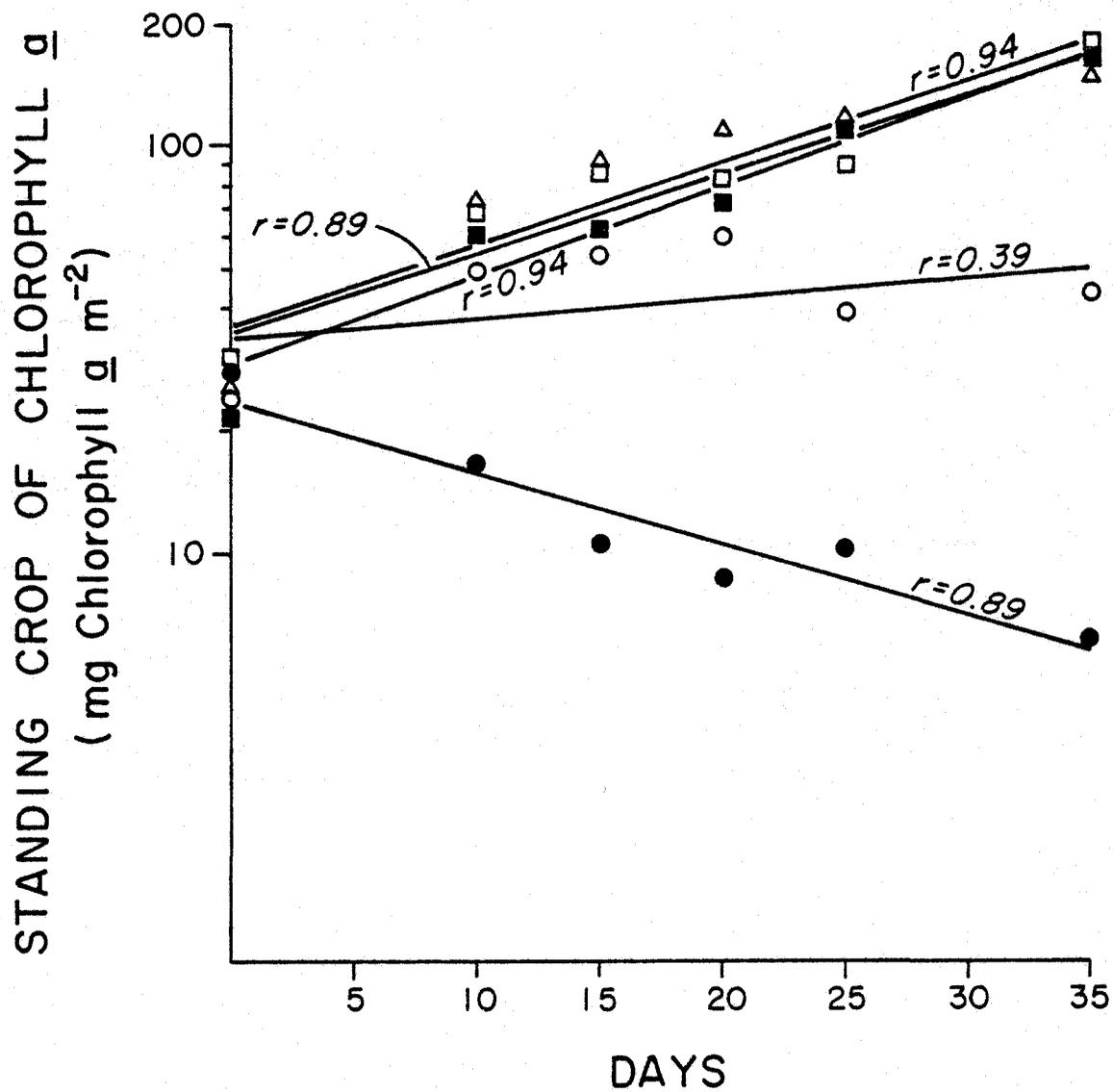


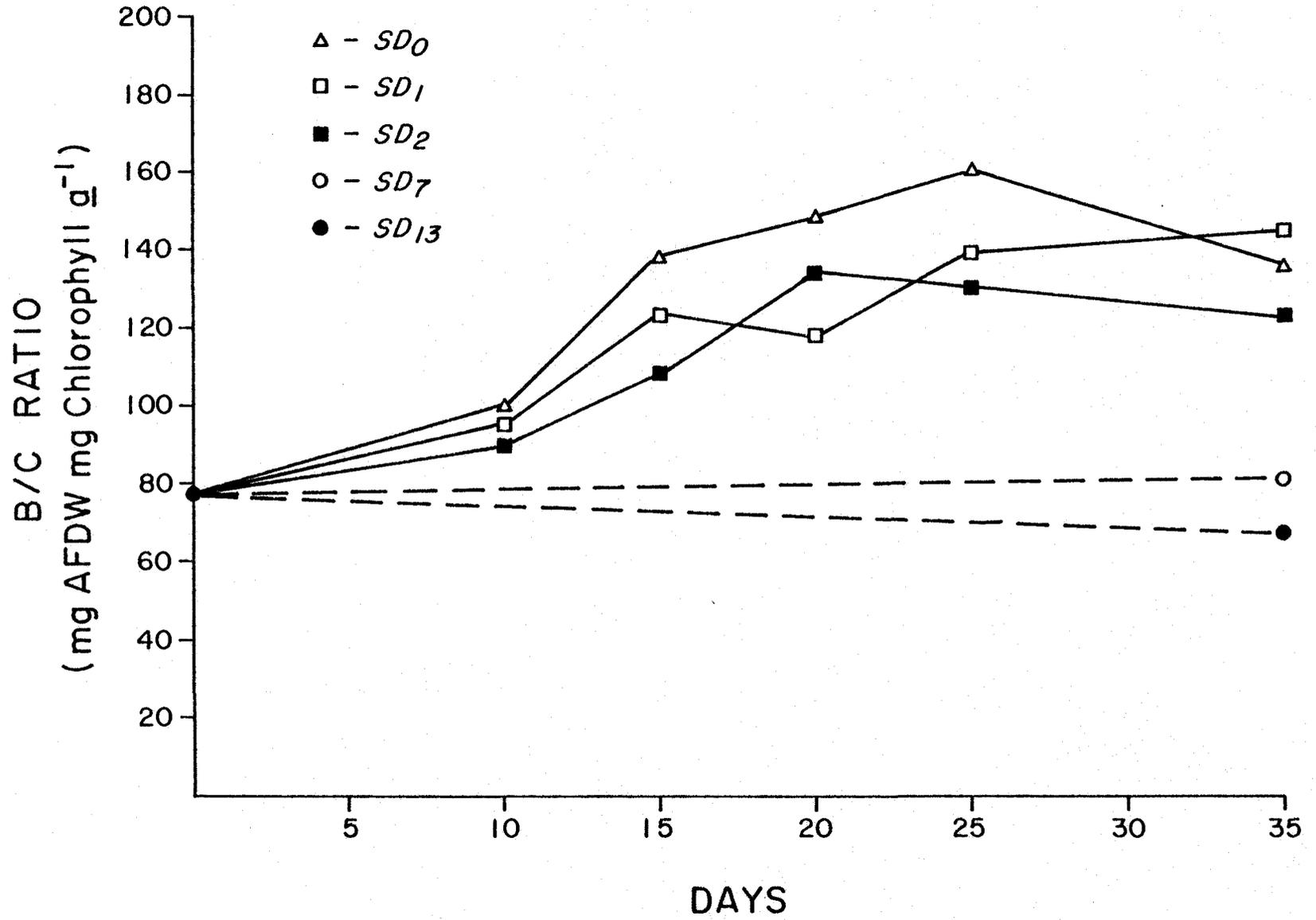
Table 2. Analysis of covariance between regressions of standing crops of chlorophyll a or biomass of periphyton through time at different grazer densities (SD_{13} - 13.26 g m⁻², SD_7 - 6.66 g m⁻², SD_2 - 2.22 g m⁻², SD_1 - 1.11 g m⁻², SD_0 - 0 g m⁻²).

Regression Comparison	d.f.	Comparison of Slopes		Comparison of Elevations	
		F		F	
Standing Crop of Chlorophyll <u>a</u>		Chla	Biomass	Chla	Biomass
SD_{13} vs SD_0	1,38	115.21***	111.51***	87.78***	87.77***
SD_7 vs SD_0	1,36	12.11***	18.24***	17.63***	25.95***
SD_2 vs SD_0	1,36	0.57 NS	0.04 NS	0.86 NS	3.52 NS
SD_1 vs SD_0	1,35	0.00 NS	0.74 NS	0.30 NS	0.15 NS
SD_{13} vs SD_7	1,42	35.49***	40.71***	73.64***	79.18***
SD_{13} vs SD_2	1,42	169.21***	252.70***	76.17***	83.58***
SD_{13} vs SD_1	1,41	154.34***	104.50***	97.25***	101.42***
SD_7 vs SD_2	1,40	21.03***	38.68***	12.88***	21.24***
SD_7 vs SD_1	1,39	15.59***	12.92***	24.11***	29.68***
SD_2 vs SD_1	1,39	0.72 NS	1.88 NS	2.92 NS	2.03 NS

*** indicates $p < 0.005$.

NS indicates Not Significant.

Fig. 12. B/C ratios of periphyton communities exposed to different grazing pressures during the 35-day study.



However, B/C ratios remained constant under heavy to intermediate grazing in Channels A and B. Therefore, differences in biomasses of primary producers as a result of grazing were greater than differences in standing crops of chlorophyll a.

Biomass of primary producers were also reduced at heavy and intermediate densities of grazers but unaffected at low densities of grazers (Fig. 13). Biomasses of primary producers at SD₀, SD₁, and SD₂ were even more elevated above those at SD₇ and SD₁₃ than was observed for chlorophyll a. Standing crops of primary producers at SD₀, SD₁, and SD₂ were 6.1 times greater than those at SD₇ and 52.7 times greater than those at SD₁₃. Heavy to intermediate grazing reduced potential standing crop of primary producers and maintained immature communities of primary producers with low B/C ratios.

Rates of primary production responded to grazing in much the same pattern as did standing crops of primary producers. Rates of gross primary production decreased slightly through time at SD₁₃ and increased at all other densities (Fig. 14). There was a significant difference in gross primary production at the different snail densities (Two-way ANOVA, Appendix E); however, there was no significant difference between gross production at day 15 and day 35, reflecting the decreases observed at SD₁₃. However, when SD₀, SD₁, and SD₂ were tested separately, there was no significant difference in rates of gross primary production. There was a significant difference in rates of gross production at day 15 and day 35, reflecting the increase in production through time at low grazing rates or no grazing. Therefore, at low grazer densities or no grazing, gross primary production

Fig. 13. Biomasses of periphyton at different grazing pressures during the 35 day study. Points represent means of samples for sampling dates.

$$(Y_{SD_0} = 3.04e^{0.063x}, Y_{SD_1} = 3.45e^{0.052x}, Y_{SD_2} = 2.30e^{0.065x}, \\ Y_{SD_7} = 2.75e^{0.011x}, Y_{SD_{13}} = 1.83e^{-0.043x}).$$

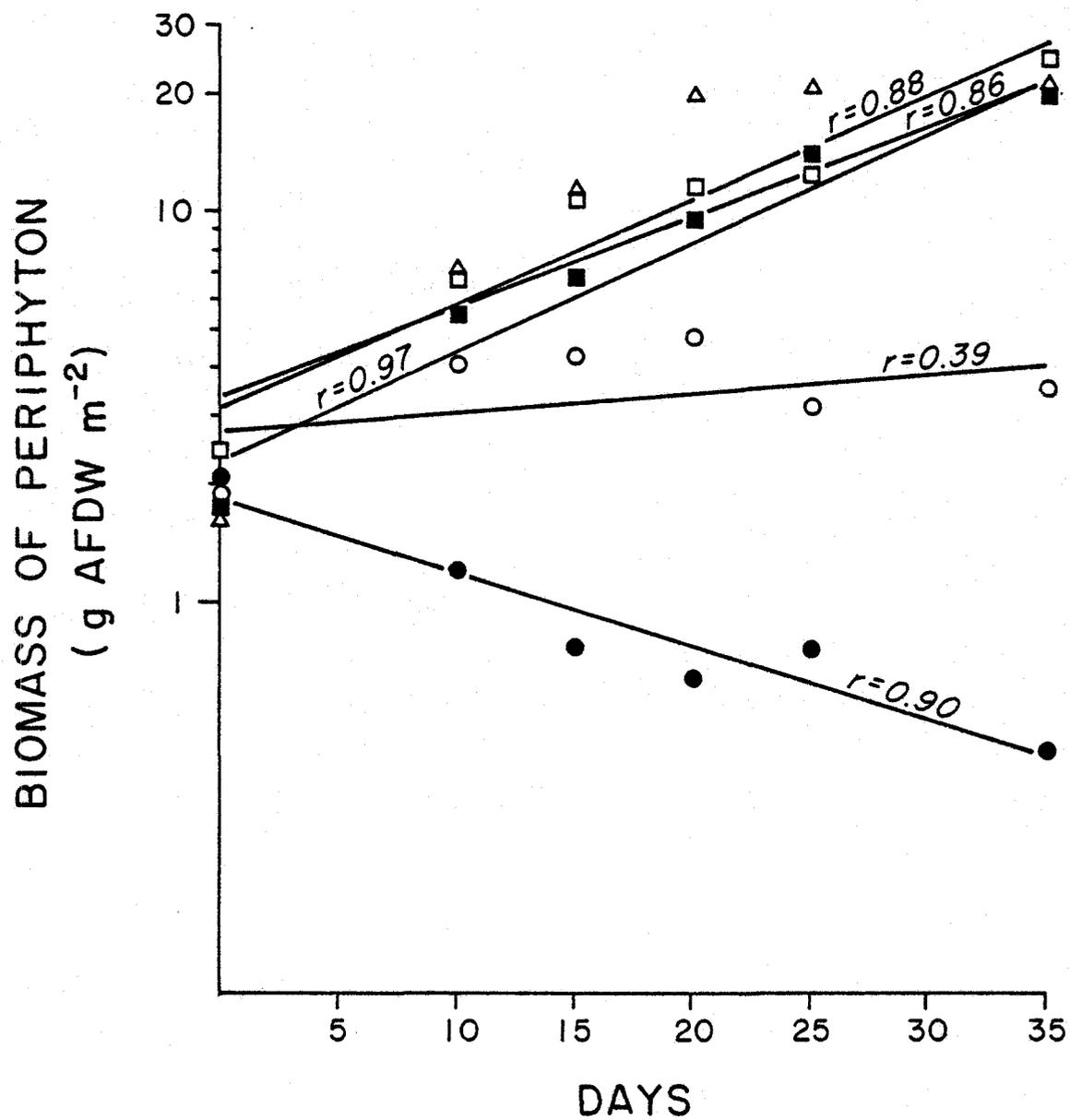
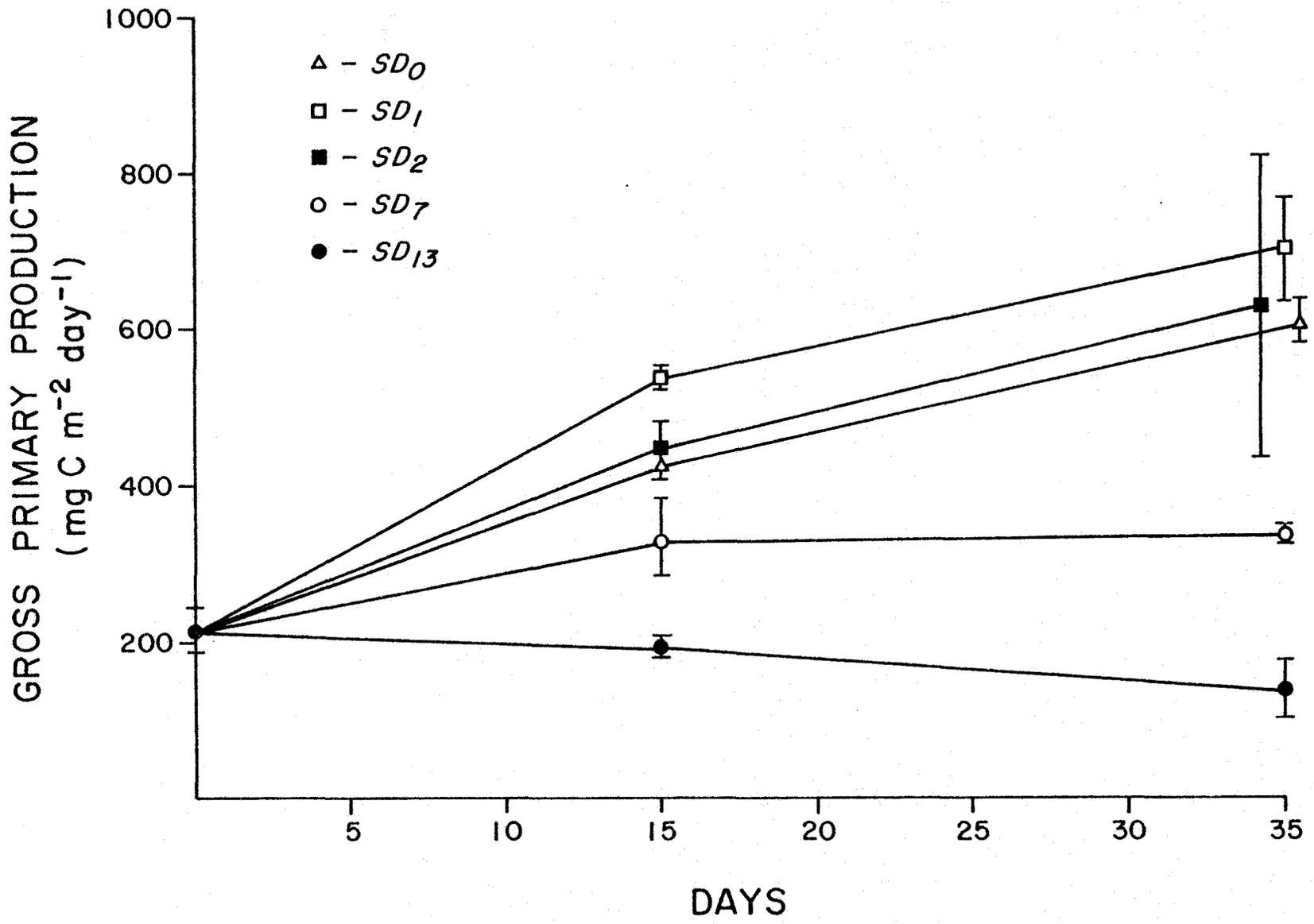


Fig. 14. Rates of gross primary production during the 35 day study in which grazing pressure was regulated at four densities of snails. Points represent means of two determinations and bars indicate ranges.



increased throughout the experiment. However, heavy to moderate grazing caused a reduction in gross primary production as compared to primary production with no grazing pressure.

Net community primary production displayed a response to grazing that was similar to the response of gross primary production (Fig. 15). Net community primary production also increased through time at SD₀, SD₁, and SD₂, maintained fairly constant at SD₇, and decreased at SD₁₃. Rates of net community primary production were significantly different at the different snail densities (Two-way ANOVA, Appendix E). At SD₀, SD₁, and SD₂ alone, rates of net community primary production were not significantly different; however, the difference between day 15 and day 35 was significantly different.

Gross primary production and net community primary production showed similar patterns largely because community respiration was not significantly different at the different snail densities (Fig. 16). There was no significant difference in community respiration at the different snail densities (Two-way ANOVA, Appendix E). Therefore, net community primary production should reflect the pattern of gross primary production.

Net daily metabolism was always positive during the study; at SD₁₃, net daily metabolism gradually decreased but it increased in all other channels (Fig. 17). Differences in net daily metabolism at different snail densities were significant; however, when SD₀, SD₁, and SD₂ were considered alone, there was no significant difference (Two-way ANOVA, Appendix E). The change in metabolism at SD₀, SD₁, and SD₂ was significant. However, grazing at high to moderate

Fig. 15. Rates of net community primary production during the 35 day study in which grazing pressure was regulated at four densities of snails. Points represent means of two determinations and bars indicate ranges.

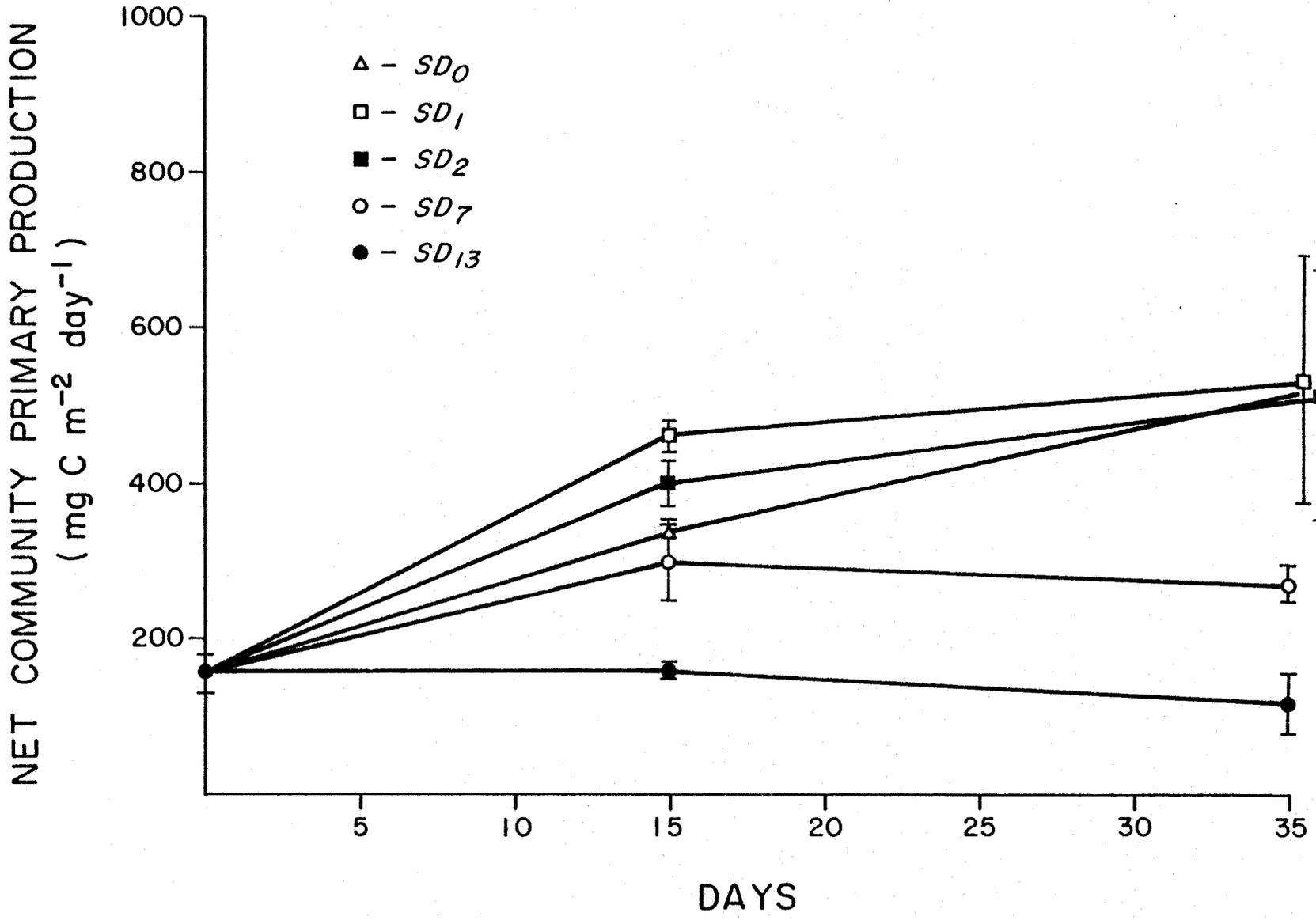


Fig. 16. Rates of community respiration during the 35 day study in which grazing pressure was regulated at four densities of snails. Points represent means of two determinations and bars indicate ranges.

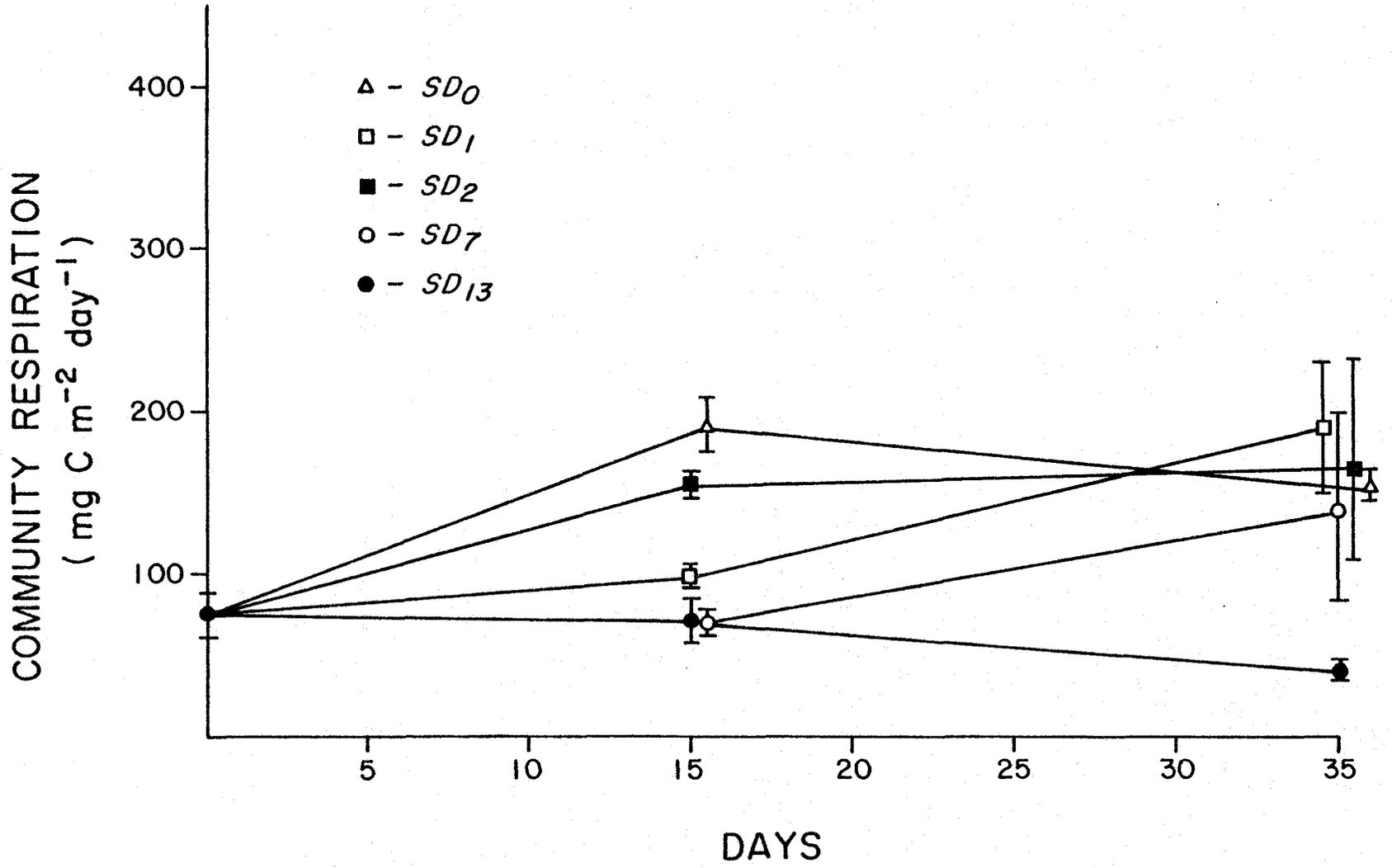
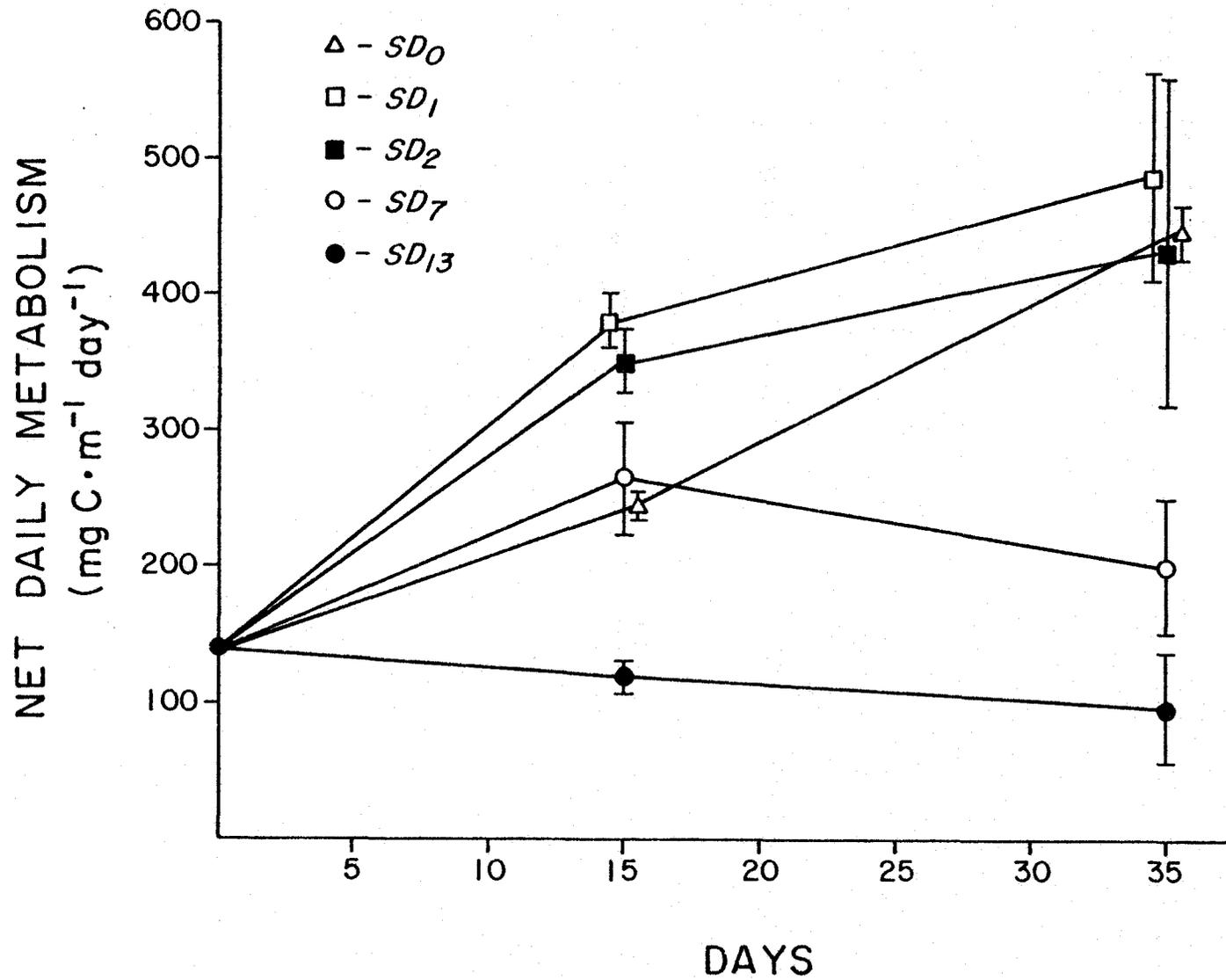


Fig. 17. Net daily metabolism of periphyton communities under different grazing pressures during the 35 day study. Points represent means of two determinations and bars indicate ranges.



densities of snails reduced potential daily metabolism, but low grazing pressure had no effect on net daily metabolism.

Turnover times (mean biomass of periphyton/net community primary production) ranged from a low of 1.45 days at SD₁₃ to a maximum of 21.75 days at SD₀ (Fig. 18). Turnover times generally increased through time at SD₀, SD₁, and SD₂, remained fairly constant at SD₇, and decreased at SD₁₃. The differences in turnover times between different snail densities were significant (Two-way ANOVA, Appendix E). However, the differences in turnover times between SD₀, SD₁, and SD₂ were not significant. Therefore, it required longer to replace the standing crop of periphyton at low grazer densities or no grazing than at high to moderate densities of grazers. Lower turnover times in the more heavily grazed systems reflected the lower standing crops of primary producers at those densities of grazers.

Patterns of primary production in the different densities of grazers indicated that the potential for production at different standing crops of periphyton was not a linear function of biomass of primary producers. Gross primary production increased as standing crops of primary producers increased (Fig. 19). However, primary production rates at low standing crops were not as depressed as might be expected. Standing crops of chlorophyll a in the control exceeded those at SD₁₃ by a factor of 26 and biomass of primary producers in the control was 52 times greater than those at SD₁₃. However, gross primary production in the control was only four times greater than that at SD₁₃. The relationship between assimilation number and standing crop of chlorophyll a clearly indicates that primary producer communities at

Fig. 18. Turnover times of periphyton communities exposed to different grazing pressures in laboratory streams during the 35 day study. Points represent means of two determinations and bars indicate ranges.

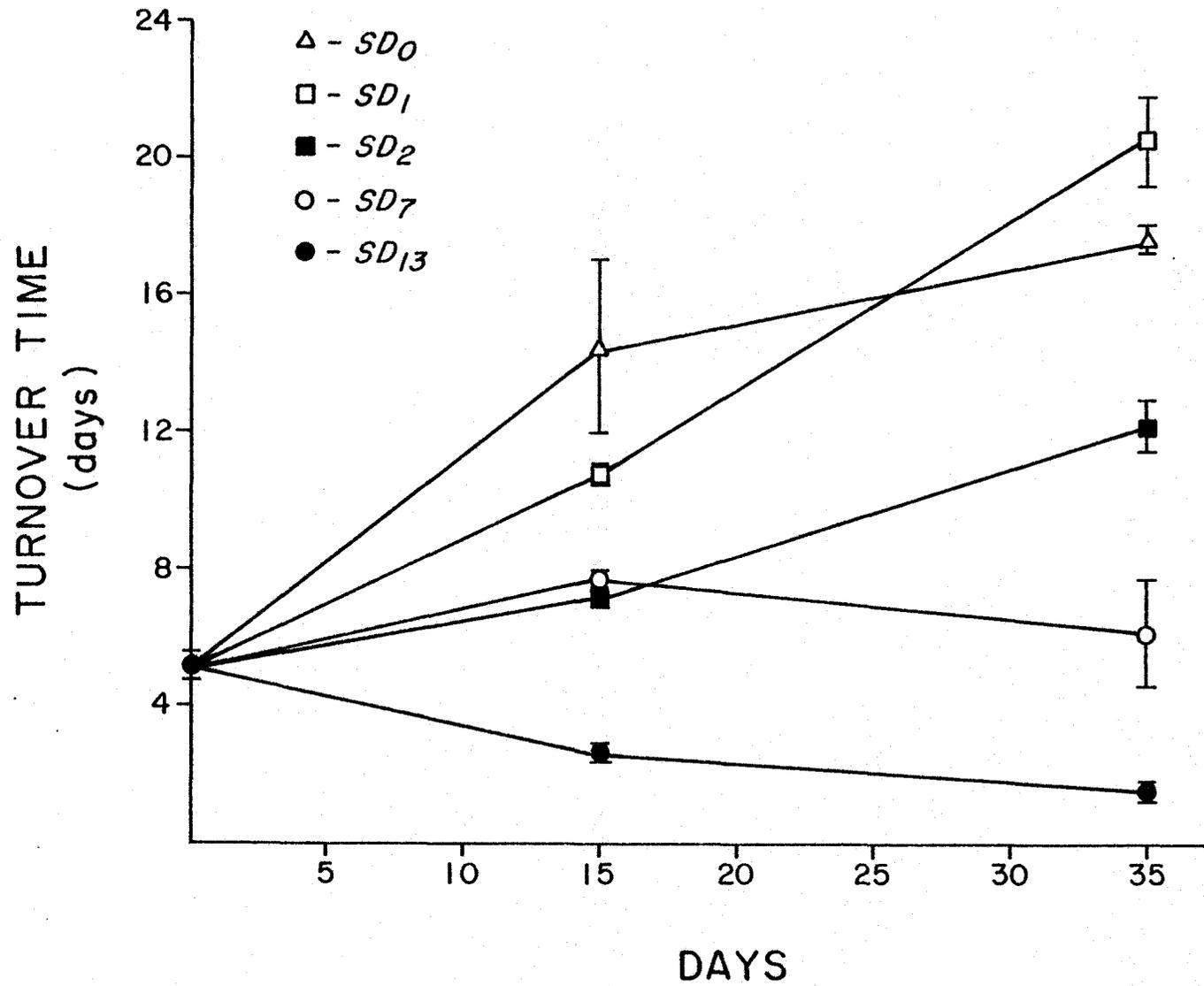
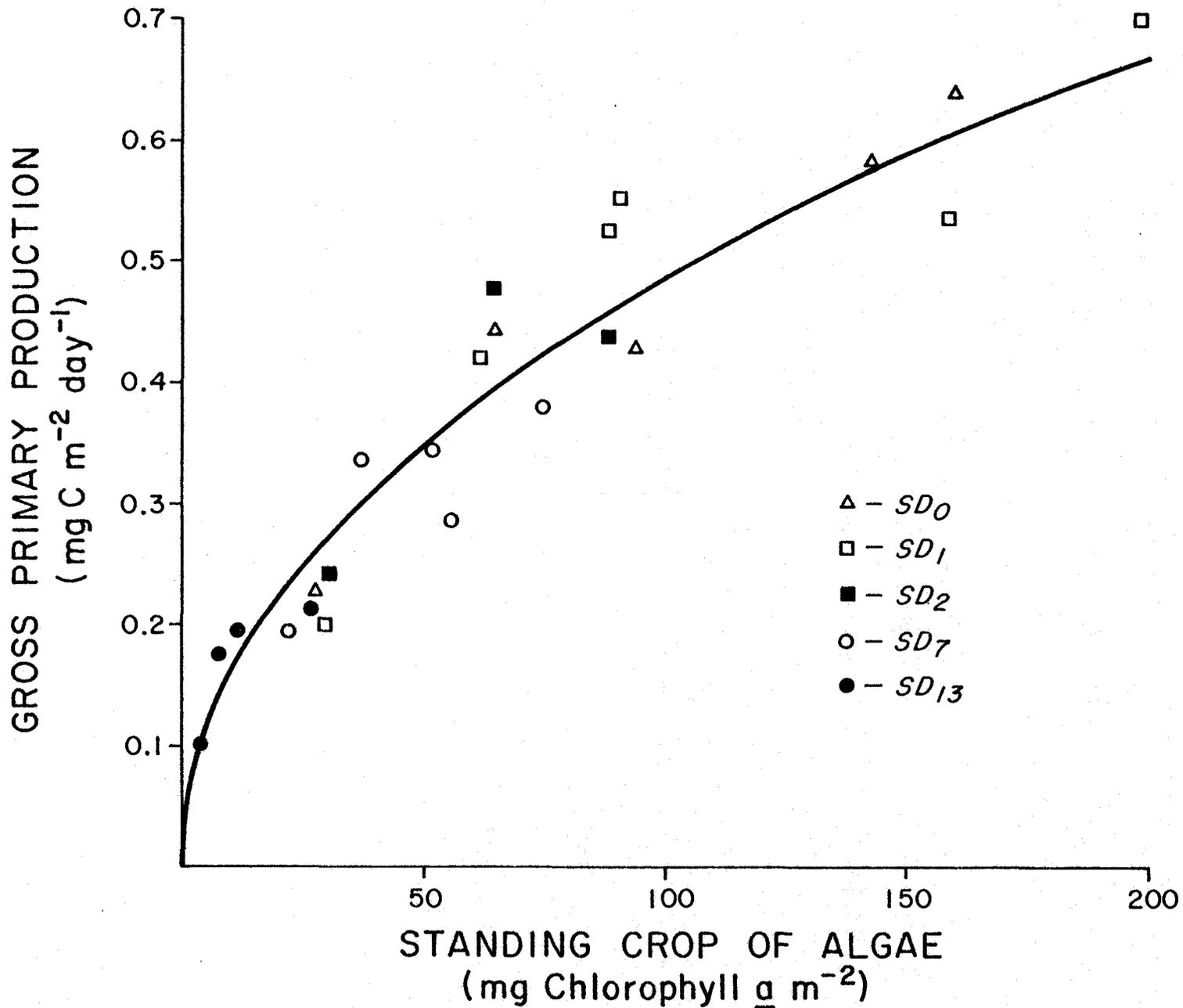


Fig. 19. Rates of gross primary production in relation to standing crops of chlorophyll a in periphyton communities exposed to different grazing pressures in laboratory streams during the 35 day study.



low standing crops had a greater production per unit weight than communities at higher standing crops (Fig. 20). At standing crops less than 50 mg chlorophyll a m⁻², assimilation number increased strongly with decreasing standing crop. The greater assimilation number at low standing crops provides a mechanism for minimizing the impacts of grazing on aquatic primary producers. As grazers depress standing crop of primary producers, the productive capacity of the primary producers is enhanced.

In addition to changes in production and standing crop, changes in pigment composition were also noted. The ratio of absorbance of an acetone extract at 480 nm to absorbance at 665 nm provides an estimate of the relative amounts of carotenoid pigments compared to chlorophyll a. High ratios are indicative of communities dominated by diatoms and low ratios are typical of communities dominated by green and blue-green algae. At SD₇ and SD₁₃, there was an initial decline after introduction of grazers, followed by a general increase throughout the rest of the experiment (Fig. 21a). At SD₀, SD₁, and SD₂, there was an increase in the ratio until the 15th day, followed by a decrease throughout the rest of the study (Fig. 21b). These patterns indicate an increase in the dominance of diatoms at SD₇ and SD₁₃. At SD₀, SD₁, and SD₂, however, there appeared to be a general increase in dominance of diatoms until the middle of the study and then a shift away from diatom dominance, possibly toward a community of green algae. Therefore, grazers were able to shift the composition of the primary producer communities.

Analysis of community structure of the periphyton by Dr. David Busch confirmed that there was a taxonomic shift in response to grazing.

Fig. 20. Assimilation number in relation to standing crops of chlorophyll a in periphyton communities exposed to different grazing pressures in laboratory streams during a 35 day study.

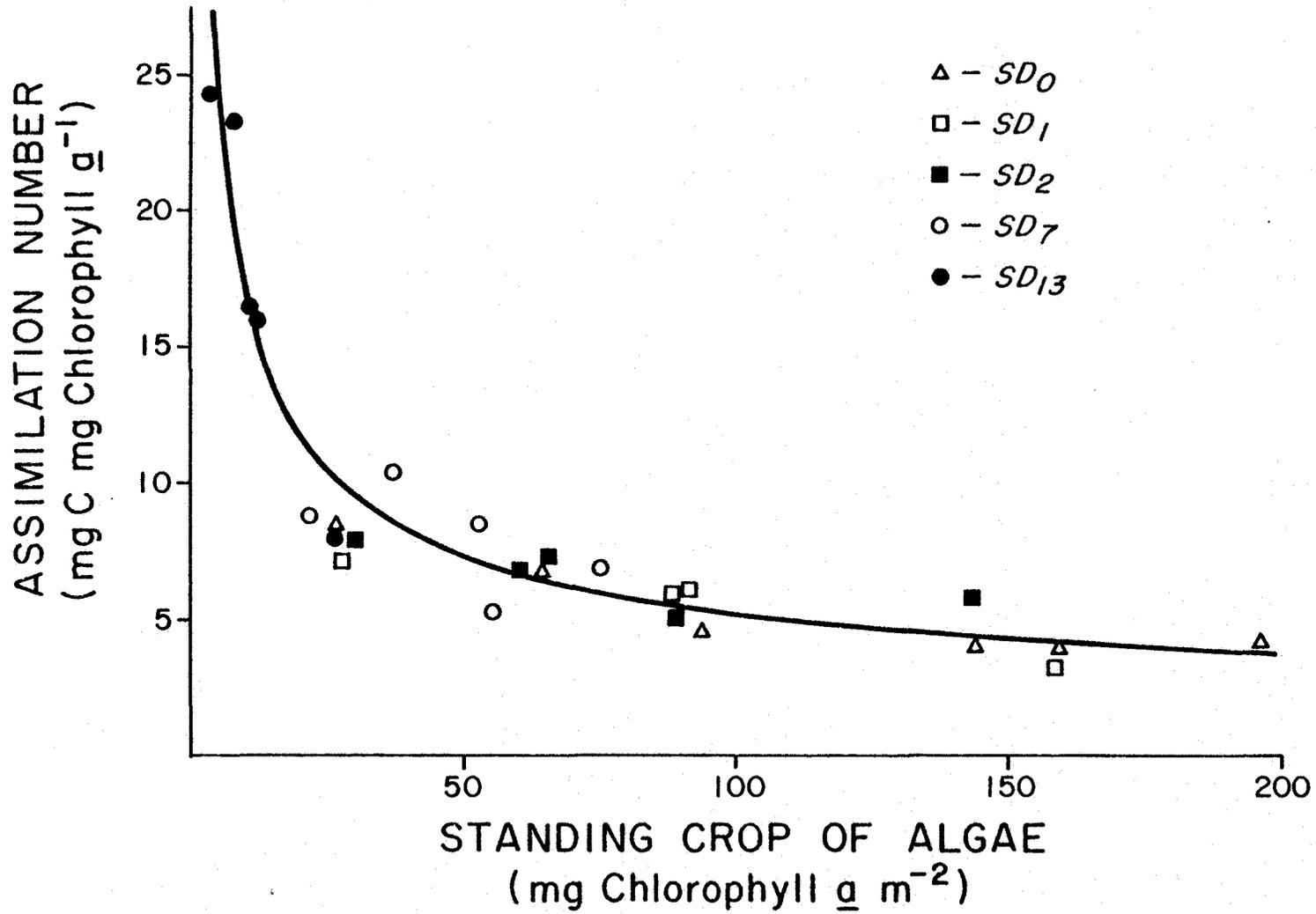
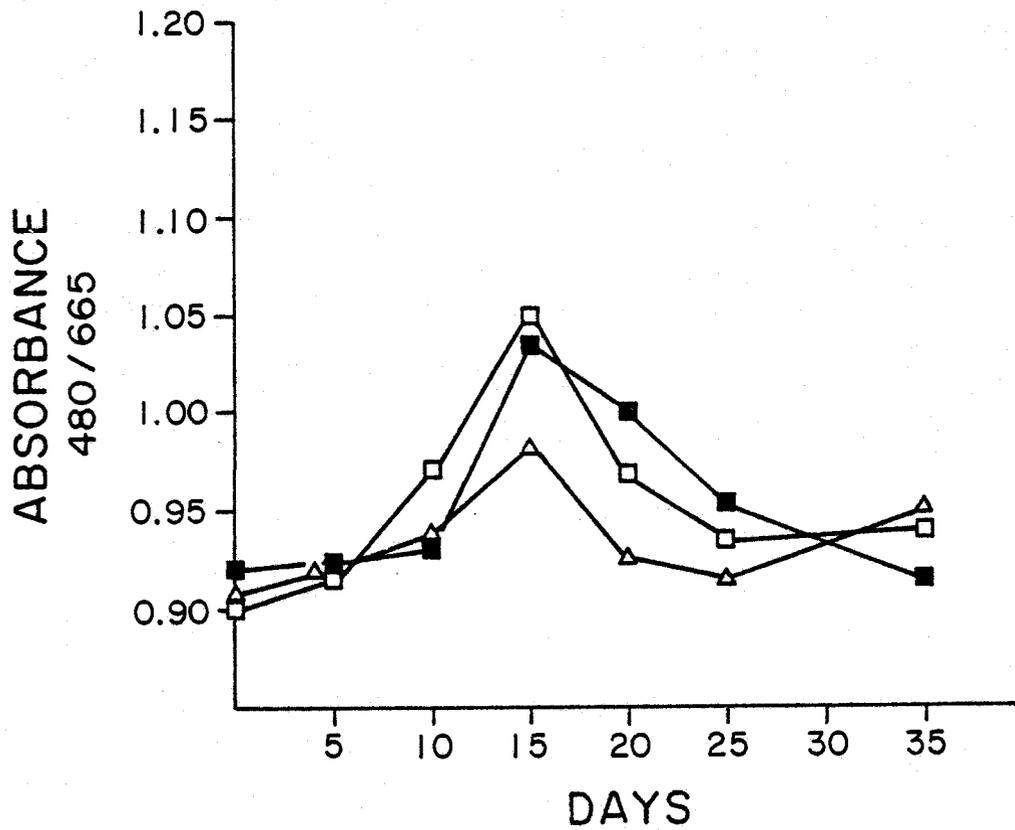
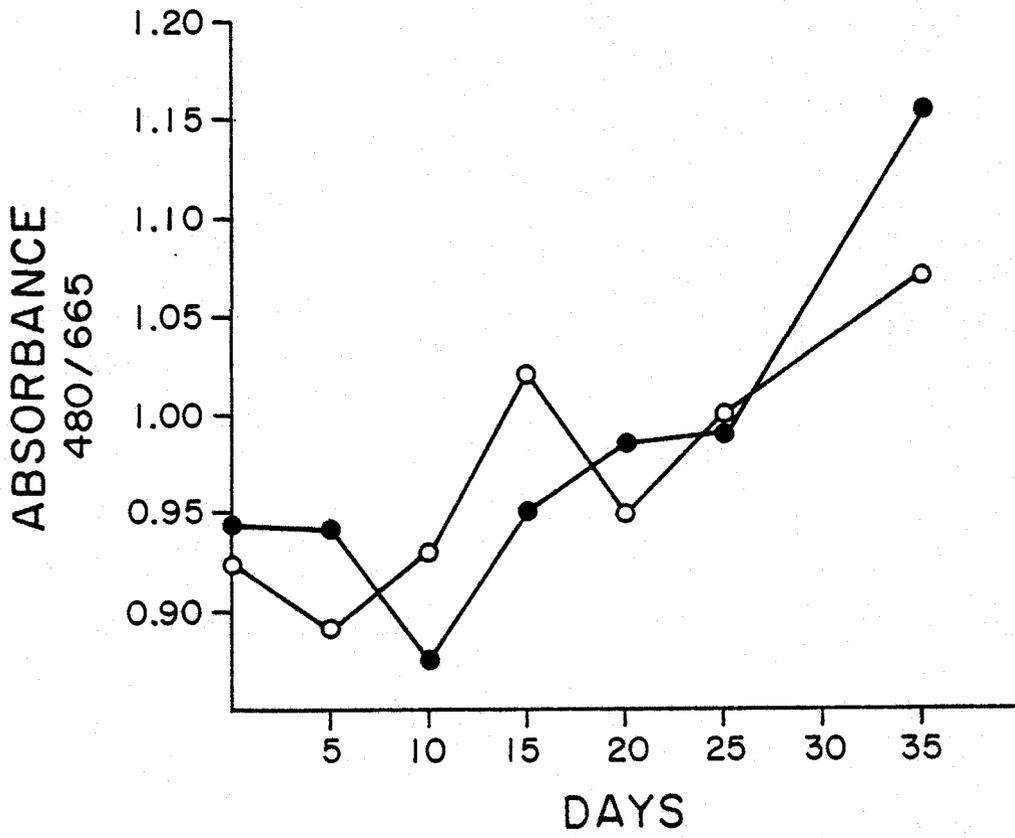


Fig. 21a. Ratios of absorbance at 480 nm to absorbance at 665 nm for heavily grazed and moderately grazed periphyton communities in laboratory streams during the 35 day study.

Fig. 21b. Ratios of absorbance at 480 nm to absorbance at 665 nm for periphyton communities exposed to two low densities of snails and no snails.



At the start of the experiment the primary producer community was mainly composed of diatoms and a filamentous blue-green alga, Schizothrix calcicola (Table 3). Ten days after the snails were introduced, a filamentous green alga, Stigeoclonium subsecundum, appeared in the channels. The ratio of Schizothrix to diatoms decreased after introduction of grazers and was inversely related to grazer density throughout the rest of the study. The ratio of Stigeoclonium to diatoms displayed a similar pattern with grazer density after Stigeoclonium appeared in the channels. In the control channel, the initial community was mainly composed of diatoms and Schizothrix, followed by a community of diatoms and Stigeoclonium, followed by a community of diatoms, Stigeoclonium, and Schizothrix. Initially, diatom communities were dominated by Achnanthes lanceolata and Navicula minuscula. After introduction of grazers, SD₇ and SD₁₃ were dominated by a smaller species of Achnanthes, Achnanthes minutissima, and SD₁ and SD₂ were mainly composed of Achnanthes minutissima, Nitzschia amphibia, and Synedra rumpens. The control channel was dominated by Synedra rumpens and Nitzschia amphibia through the 20th day and shifted to a community mainly composed of Achnanthes lanceolata and Navicula minuscula thereafter. The observed changes in species composition are consistent with shifts of pigment structure in the periphyton as a result of grazing. Heavy to intermediate grazing resulted in communities dominated by diatoms; heavy grazing led to the dominance of a smaller species of diatom. Low grazing pressure resulted in communities that closely resembled ungrazed communities.

Table 3. Proportions of Stigeoclonium and Schizothrix to diatoms at different densities of grazers at 0, 15, and 35 days after introduction of grazers. All values are expressed as microns per diatom.

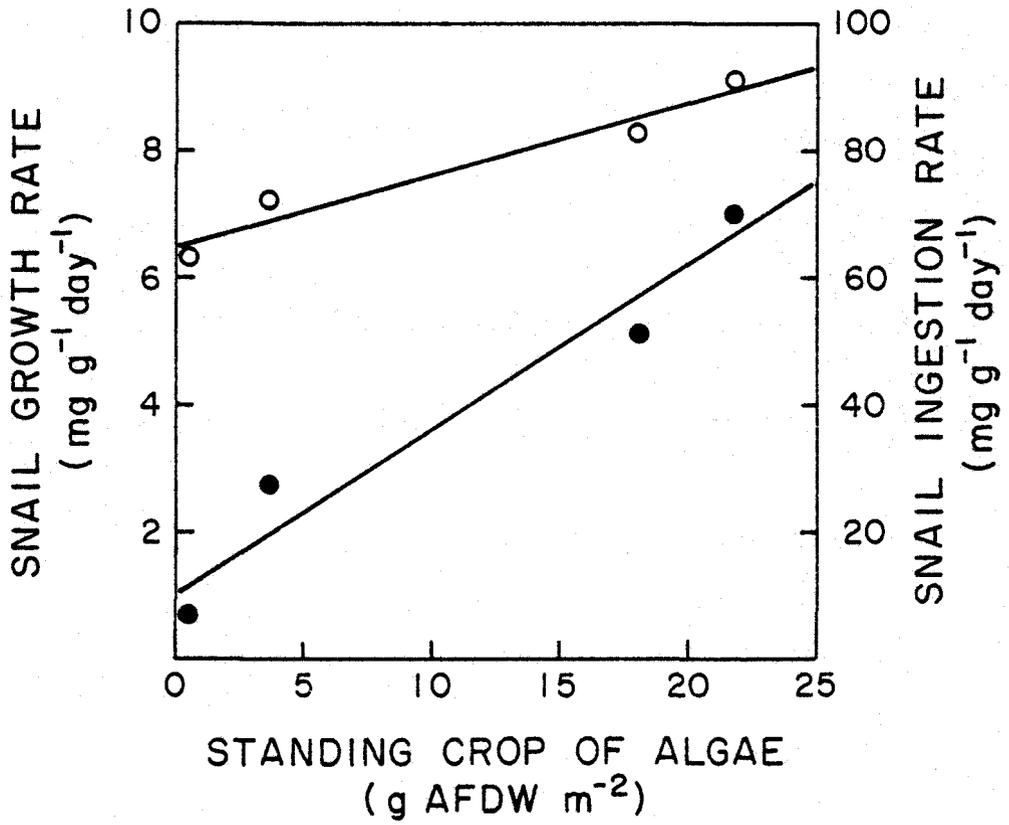
	0	Day 15	35
<u>Stigeoclonium/diatom</u>			
SD ₁₃	0	0	0.2
SD ₇	0	0.5	0.2
SD ₂	0	0.5	2.0
SD ₁	0	0.7	3.4
SD ₀	0	2.5	1.2
<u>Schizothrix/diatom</u>			
SD ₁₃	11.6	2.6	1.9
SD ₇	8.6	6.8	5.3
SD ₂	13.9	6.0	12.8
SD ₁	10.5	11.6	9.4
SD ₀	8.3	5.3	8.3

Grazers also influenced their own metabolism through modification of their prey. In the artificial channels, grazers were not able to adjust to changes in availability of their prey by altering their own densities. The ingestion rate of the snails at SD₁ was 44% greater than that at SD₁₃; ingestion rate increased with increasing standing crop of primary producers (Fig. 22). McCullough noted as he was measuring ingestion rates that variability of the estimates was greatest when the snails were feeding on substrates from the channels with low densities and least on substrates from the channel with high density of snails. It appeared that snails had to continually feed at the low standing crops of primary producers and, therefore, estimates of ingestion were consistent. At high standing crops of algae, the feeding activity of the snails was erratic, probably as a result of the ease with which they could obtain enough food for satiation. Snails had positive growth rates at all grazer densities; however, growth rates were greater at higher standing crops of primary producers (Fig. 22). Growth rate of the snails at the lowest snail density was 11 times greater than the growth rate at the highest density of snails. Therefore, at fixed densities, grazers limited their own growth and ingestion by reduction of primary producer biomass with increasing densities of grazers.

Discussion

Particular characteristics of both grazers and primary producers influence their interaction in lotic systems. There are many types of grazers: raspers that grind off the periphyton, scrapers that detach

Fig. 22. Rates of growth (O) and ingestion (O) by snails in relation to standing crops of periphyton at the end of the 35 day study. (For growth rates, each point represents the mean of 20 individual estimates and bars indicate one standard deviation. For ingestion rates, each point represents the mean of 3 individual estimates and bars indicate one standard deviation) (data obtained from Dale McCullough, Oregon State University).



periphyton with blade-like appendages, collectors that feed on the loosely attached material on the surface of periphyton, browsers that pluck at clumps of periphyton and filamentous algae, and piercers that suck protoplasm out of large algal cells (Cummins 1978). Distributions of the many aquatic invertebrates that feed on algae are controlled by the anatomy and physiology of the organisms, current, substrates, light, food resources, competition with other invertebrates, and predation. The ability of grazers to handle their prey is influenced by the growth form of the periphyton, such as monolayers of unicellular algae, filamentous algae, colonial masses, leafy sheets, crustose forms, or mats of unicellular algae. Cell size of the algae may also affect handling ability. Digestability of algae may vary depending on cell wall structure, presence of silica frustules in diatoms, and toxic or noxious substances (Hargrave 1970, Calow 1973, Carmichael et al. 1975, Porter 1978). The response of the algae to grazing is a function of physiology of the taxa, age of the community, and physical factors that regulate rates of primary production (Calow 1973). Thus, interactions between grazers and primary producers may yield a wide range of responses as a result of many factors, including type of grazer, distributions of grazer populations, growth forms of the algae, digestability of the algae, and productivity of the periphyton.

Herbivory involves more than simple reduction of standing crop of primary producers; it may alter community structure, allow the development of a particular growth form, change the age structure of the community, or increase nutrient availability by rupturing cells and excreting wastes. In terrestrial ecosystems it has been known

for some time that grazing, particularly by ungulates on grasses, may actually stimulate primary production. McNaughton (1979) reviewed grazing as an optimization process and, though he found abundant data to support the concept, warned that simple statements about the effects of herbivores on plant systems were "fraught with errors."

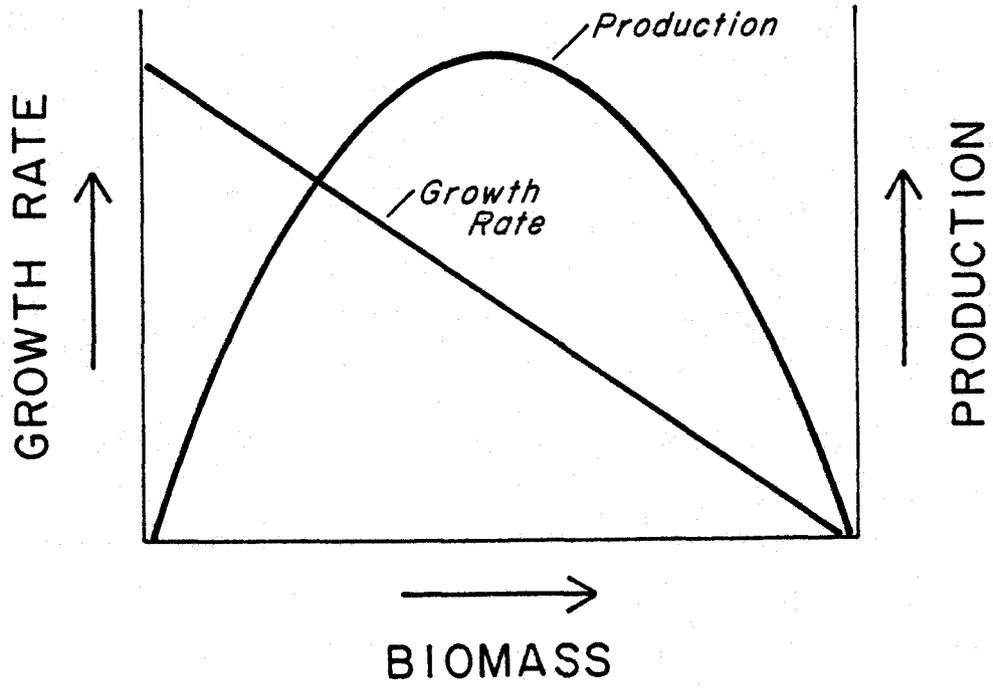
Evidence for stimulation of primary production by grazing has been found in aquatic systems, but only in lentic systems. Net community primary production of epibenthic algae in Marion Lake was stimulated at low densities of amphipods (Hargrave 1970). As amphipod densities increased, the trend reversed and primary production was lower than that on ungrazed substrates. In aquaria, herbivorous minnows were allowed to graze on periphyton for 20 days (Cooper 1973). At the end of the experiment, net community primary production was enhanced with increasing herbivore biomass up to a certain density and increased beyond that density. Crayfish in Lake Tahoe were observed to stimulate primary production of periphyton (Flint and Goldman 1975). At crayfish biomass greater than 203 g m^{-2} , primary production was inhibited; however, at crayfish biomass less than 131 g m^{-2} , primary production was enhanced. All three above-mentioned studies found that primary production could be stimulated by grazing, but that the stimulatory effect could be overridden by excessive consumption at high densities of herbivores.

Nutrient regeneration or excretion by grazers and cropping to juvenile communities are possible mechanisms for stimulation of primary production by grazing. Cooper (1973) suggested that nutrient regeneration or grazer excretion was the cause of the stimulation of

primary production that was observed in his studies with Notropis. Nutrient release by the rupturing of cells during feeding is a potential source of stimulation. Also, excretions or secretions of the grazer may stimulate primary production. Many grazers in streams are streamlined so that they stay as close to the boundary layer as possible. This form of association of the grazer with the substrate would maximize the potential for nutrients released during grazing to remain in the boundary layer around the periphyton community. Cropping may also cause an apparent increase in primary production by reducing standing crops of primary producers to a more productive biomass. This is basically a logistic growth system (Fig. 23). As biomass increases, growth rate decreases. Production, the product of biomass and growth rate, would then be maximum at an intermediate biomass. Therefore, if grazing reduces high biomasses of primary producers to intermediate biomass, production may be increased. Reduction of periphyton communities to extremely low standing crops would decrease production. The model that was used as an example assumed that the decrease in growth rate with increasing biomass was linear. In my study, assimilation number of the periphyton decreased exponentially with increasing biomass; therefore, maximum primary production would occur at even lower standing crops. Therefore, primary producers in streams are well adapted for sustaining heavy grazing pressure.

In lotic systems, evidence for stimulation of primary production by grazers has not been found; however, grazers have been shown to regulate standing crops of benthic algae. Increased abundance of

Figure 23. Hypothetical relationships between biomass, growth rate, and production. From Warren 1970.



grazers was followed by a decrease in numbers of Achnanthes lanceolata in an English stream (Douglas 1958). After an application of DDT to a stream eliminated all aquatic insects, periphyton standing crops increased (Ide 1967). In Africa, an insecticide from cattle dipping tanks was released to a stream and destroyed the entire fauna (Chutter 1970). Standing crops of periphyton increased immediately after the release; as the fauna recovered, standing crops of periphyton decreased to prepoisoning levels. Therefore, grazers may play a major role in regulating quantities of periphyton in streams.

Reduction of standing crop of periphyton is a basic effect of grazing that would be expected because of cropping action. In my study, periphyton biomass was reduced with heavy to intermediate grazing, but no significant reduction was observed at low densities of grazers. Previous studies have also found that grazers were capable of reducing standing crops of periphyton (Beyers 1963, Dickman, Cooper 1973, Flint and Goldman 1975). Grazers were found to be responsible for maintenance of equal quantities of primary producers in three artificial stream channels that received different levels of nitrate enrichment (Speir 1979). Effects of grazing by another aquatic snail, Physa gyrina, on primary production was observed in laboratory streams (Kehde and Wilhm 1972). In two laboratory channels there were no grazers and in two other channels snail densities of 120 snails m^{-2} with biomasses of 15.6 $g\ m^{-2}$ were established. These snails were approximately ten times larger than the Juga in my study, so biomass of snails in their grazed sections was similar to the highest density of snails in my experiment though the numbers were lower. They observed no significant difference

in standing crops of periphyton biomass between the grazed and ungrazed channels, a surprising result in view of the snail densities used. In general, grazing can reduce standing crops of periphyton but there may be no effect at low densities of grazers.

Because grazers can influence the standing crop and maturity of periphyton communities, they can also affect B/C ratios. In my study, B/C ratios were higher at low densities of grazers or in ungrazed sections. The communities dominated by diatoms in the heavily grazed channels had lower B/C ratios than the more mature communities in the channels with low densities of grazers. Low grazing pressure allowed the development of older, filamentous communities, which would be expected to have lower concentrations of chlorophyll. Kehde and Wilhm (1972) also observed higher B/C ratios in the ungrazed sections. As a result of the difference in B/C ratio, standing crop of chlorophyll a was significantly greater in the grazed sections, a relationship not observed in my study.

Direct stimulation of instantaneous rates of primary production was not observed in my study except for the channel with the lowest density of grazers on the 15th day. However, low grazing intensity was supported with no significant reduction in standing crop or productivity of primary producers. Differences in total production between treatments may have been masked by consumption and export of primary producers. A material balance approach would incorporate these losses. Total production of primary producers is equal to accumulation of biomass and primary producers, export of primary producers and consumption of primary producers. Such an analysis may reveal

differences in primary production that are not evident in estimates of instantaneous rates of primary production.

Total primary production was lowest at the intermediate and high density of snails (Table 4). However, there was no major difference between the total production in these two channels even though the grazing pressure was measured to be 75% greater at the high density of snails. There appeared to be slightly greater production at the lower grazer densities than in the ungrazed channel. However, standing crops of periphyton in these channels were patchy (standard deviations at the end of the study at SD_0 , SD_1 , and SD_2 were 29%, 19%, and 17% of the mean standing crop, respectively); therefore, differences between total production in the channels with low densities of grazers and the ungrazed channel would not be statistically significant. Only in one case in the 15th day was there evidence for stimulation of primary production. The material balance suggests that total production was slightly greater at low densities of grazers but that cannot be supported statistically. However, both of these measures demonstrated that there was a compensatory mechanism that allowed primary producers to support higher grazing pressures. Primary production was not reduced as much as would be expected from the consumptive demand of the grazers. Grazing maintained young, monolayer communities dominated by diatoms in the channels with high and intermediate densities of snails. Communities of primary producers in the channels that had low densities of snails or were ungrazed developed older, thicker growth forms, dominated by filamentous algae and epiphytic diatoms. The younger, monolayer communities were more productive per unit weight than the

older, thicker communities. The greater productivity of periphyton exposed to high grazing pressure provided partial compensation for the greater grazing demand.

Table 4. Total primary production in channels with different densities of grazers during a 35-day study. All values are expressed as g AFDW m⁻².

Channel	A	B	C	D	E
Accumulation of biomass	-1.32	1.58	18.14	23.44	18.52
Export	3.58	4.10	2.87	0.92	0.92
Consumption	11.72	6.75	2.89	1.43	0
TOTAL	13.98	12.43	23.90	25.79	19.44

A simulation model of periphyton dynamics in laboratory streams incorporated a grazer process patterned after the snail used in my study (McIntire 1973). Results derived from this model indicated that grazers should be able to reduce standing crops of periphyton and maintain them at low levels. The model also demonstrated that low standing crops of periphyton could support biomasses of grazers 20 times greater than their own because of the short turnover times of the periphyton. McIntire's model predicted that periphyton communities could support consumer biomasses more than 20 times greater than their own. I found that standing crops of periphyton as low as 0.49 g m⁻² supported standing crops of snails of 10.08 g m⁻² and the snails maintained positive growth rates. Standing crops of the consumer were 20 times greater than that of their prey, as McIntire's model

predicted was possible. These results support the concept of the inverted pyramid of biomass; low biomasses of periphyton can support much higher standing crops of consumers.

Grazing may prevent the development of particular species or may select for certain species, thereby changing species composition of the periphyton. In my study, diatom communities were present in the channels with high densities of grazers but communities of filamentous algae and diatoms were present at low grazer densities. Snails in a microcosm study shifted community structure from a community dominated by filamentous algae and macrophytes, Oedogonium and Vallisneria, to one comprised mainly of diatoms (Beyers 1963). The proportion of filamentous algae in the periphyton decreased in direct relation to tadpole density in a study by Dickman (1968). However, Kehde and Wilhm (1972) found no effect of grazing on diversity of primary producers in laboratory streams. In my study, high to intermediate levels of grazing altered community structure of periphyton, but low densities of grazers had little effect.

Not only do densities of grazers affect primary producers, but densities of primary producers also affect grazers. In my study, growth rates and ingestion rates of snails were directly related to standing crops of periphyton. Densities of aquatic insect larvae were found to be regulated by the removal of food from substrates after spates (Brennan et al. 1978). Drift of Baetis rhodani, a mayfly, was lacking at high standing crops of periphyton in a laboratory stream (Bohle 1979). Mayflies were concentrated on substrates with high standing crops of periphyton. Depletion of the algae resulted in

increased drift and random distribution of the grazers. Anderson and Cummins (1979) reported that weights of final instars of Glossosoma nigrion, a caddisfly, increased as the P/R ratio of stream reaches increased. This relationship suggested that growth of the insect was related to availability of primary producers.

In a subsequent study in the same laboratory streams used in my study, the interactions of grazers with primary producers at different levels of production were investigated and different responses than I observed were found (Sumner 1980). One set of channels in Sumner's study was shaded, one set was lighted (similar to the light level used in my experiment), and one set was both lighted and enriched with nitrate. Grazer densities of 500 snails m^{-2} , 125 snails m^{-2} , and 0 snails m^{-2} were established in each set of channels. These snail densities were similar to SD_7 , SD_2 , and SD_0 in my study. There were major differences between the two studies and these differences can best be understood by comparing the experiments as a whole. Therefore, I will compare and contrast the two experiments rather than integrate the various results throughout my discussion.

Several similar responses were observed in my study and the experiment by Sumner (1980). In both studies, grazing altered the community structure of the primary producers. In the grazed sections, relative abundances of diatoms increased and relative abundances of blue-green algae decreased. In Sumner's study, biomass and chlorophyll a values were less in the grazed sections; in my study, biomass and chlorophyll a values were less at SD_7 than in the control but there was no significant difference between the control and SD_2 .

Sumner's (1980) study and my study differed in several major respects. Sumner found that grazing did not significantly alter rates of gross primary production and community respiration; I found that rates of gross primary production and community respiration were significantly lower at SD₇ than in the control but there was no effect of grazing at SD₂. Ingestion of the periphyton by the snails in Sumner's study accounted for less than 20% of the energy losses from all grazed sections; in my study, grazing accounted for more than 50% of the total primary production at SD₇ but less than 15% at SD₂. In addition, Sumner found that snail growth was not directly related to biomass of periphyton; however, I found that snail growth rates increased as biomass of periphyton increased. Sumner attributed the lack of a direct relation between snail growth and periphyton to inhibition of snail growth by blue-green algae.

The experiments of grazing effects on primary producers by Sumner (1980) and me were different in several ways and these differences may have partly caused the different responses observed. Sumner's study was conducted from June through August and my study was conducted from September through October. The average temperatures during most of Sumner's study ranged from 15°C to 18°C but there was a three week period in Sumner's study when temperatures ranged between 22°C to 24°C; the temperatures in my study ranged from 10°C to 16°C. In laboratory streams at the Oak Creek Laboratory of Biology, plant communities were mainly composed of diatoms in the period from early fall through winter but during summer months the plant communities were composed of approximately equal portions of diatoms and other algae (McIntire and

Phinney 1965). Sumner used plexiglass plates for substrates and I used brick field tiles. These differences, especially the seasonal differences in community structure and temperature, may have resulted in different metabolic activity of either the primary producers or the snails. The interaction between grazers and primary producers is regulated by a complex matrix of physiological and taxonomic factors; therefore, simple and absolute relationships should not be expected.

Grazing is more than simple removal of algae; it involves interactions between biota and incorporates the complexity of living systems. If grazers are food limited, alteration of their prey will also affect them. A model of stream ecosystem processes predicted that the process of grazing would be almost entirely food limited throughout the year (McIntire and Colby 1978). Growth of the grazer in my study was limited by the availability of periphyton. It is possible for grazers to regulate densities of primary producers in streams and evidence exists for regulation of grazer density and growth by the availability of periphyton. Therefore, grazing in streams must be viewed as an interactive process that may play an important role in determining the structure and function of stream ecosystems.

OLD-GROWTH - CLEARCUT COMPARISON

In the Pacific Northwest, timber harvest is a major land-use practice that has a high potential for affecting primary production in streams. The forest canopy is usually completely removed and the amount of solar radiation reaching the stream is increased. After 10 to 20 years, the stream is shaded once again by vegetation. Potential for primary production in streams will be maximal after the initial disturbances of logging are over and channels have restabilized. I compared primary production in a paired clearcut and old-growth forest site on a third-order stream in the Cascade Mountains of Oregon to examine the response of aquatic primary producers to canopy removal.

Methods

Environmental factors that would affect primary production were measured in Mack Creek at each sampling date. These measurements were correlated to continuous measurements taken at the H. J. Andrews Experimental Forest meteorological station and the Lookout Creek gauge station. Regression equations were used to calculate annual patterns of light, temperature, and discharge for Mack Creek. Precipitation was measured continuously at the H. J. Andrews Experimental Forest meteorological station.

Primary production and related processes were measured in the old-growth forest and clearcut sections of Mack Creek at monthly intervals for one year from November 1974 to October 1975. This interval was chosen because it encompassed a water year, starting at

the beginning of the rainy season and ending just after the dry season. Samples were not taken in January and March because of inability to reach the site due to snow, and primary production was not measured in July because the pH meter malfunctioned.

Primary production was measured by total inorganic carbon measurement in a modified, McIntire primary production chamber as described in Chapter II. Rocks were collected from the stream and placed in the chamber so that the entire chamber bottom was covered. Substrates were collected so that the full range of sizes (excluding boulders or fines) was utilized. Because most of the stream was made up of intermediate riffles, substrates were collected from these areas rather than distinct pools or riffles. Only one chamber was available; therefore, a single estimate was obtained for each study section each month.

Benthic metabolism was measured by closure of the chamber for a time interval; change in concentration of carbon in the water at the end of the time provided an estimate of the rate of metabolism. The time interval of closure was arbitrarily determined as a function of light intensity, water temperature, and biomass of primary producers. Bubble formation within the chamber served as a visual indicator of the influence of these factors. Gas bubbles formed on the surface of the chambers if the concentration of oxygen or carbon dioxide greatly exceeded saturation. It is important to keep supersaturation at a minimum. If either oxygen or carbon dioxide is depleted, the rate of metabolism may be limited. Also, if a dissolved gas goes into

atmospheric phase, it is undetectable and estimates of metabolism would be in error.

Substrates were removed from the chambers and additional samples were taken from the stream for estimates of standing crops of primary producers. After 24 hours of measurement, substrates were removed from the chamber and kept in the dark at stream temperature or in the snow during winter. Two additional substrate samples were taken from each site according to the procedure previously described. Therefore, three samples were available for measurement of standing crop of chlorophyll a. These samples were transported to Oregon State University on ice and stored in a freezer for up to 3 days. The entire sample was soaked for 24 hours in darkness in a 90% solution of basic acetone at 4°C. Fifteen ml of the solution were centrifuged for 5 minutes and decanted. Absorbance was read on a Beckman Model DB Spectrophotometer at 665 nm and 750 nm. After addition of 0.1 N HCl absorbance was read again at 665 nm and 750 nm. The amount of chlorophyll a present was calculated by equations described by Wetzel and Westlake (1969). Estimates of chlorophyll a were converted to biomass of periphyton by the biomass/chlorophyll a ratios developed for the forested and clearcut sections of Mack Creek by Lyford and Gregory (1975).

Estimates of chlorophyll a and biomass were expressed on a substrate area basis. Rock substrates were wrapped with aluminum foil, avoiding overlap of the foil. Aluminum wrappings were combined for each sample and weighed; total weight was converted to area of substrate by multiplication by the area of aluminum per unit weight of foil. Rocks were removed from Mack Creek and the extent of algal growth was marked;

periphyton covered almost exactly half of the total substrate surface. Therefore, area of substrate determined with aluminum foil wrapping was converted to area of colonized surface by multiplying by 0.5. Estimates of chlorophyll a and biomass were converted to standing crops by dividing by colonized substrate area. This measure based on substrate area provided the best comparison of standing crop between the two sites, but standing crop of primary producers based on planar area of stream surface is also a useful measurement for certain comparisons. Substrate area of substrates in the chamber was divided by the planar surface area of the chamber to develop a conversion factor from substrate area to planar area of stream surface. The ratio of total colonized area to planar surface area in this study was 1.60 ± 0.08 . This ratio is less than might be expected; Nelson et al. (1969) found a ratio of 4.4 in experiments with ^{32}P uptake in Walker Branch, Tennessee. The difference can be explained by two factors: (1) the substrates in the chambers were not packed as densely as natural hydraulic packing, and (2) ^{32}P uptake in Walker Branch included uptake into total substrate area. If the latter factor is correct, the ratio can be adjusted by multiplying by 0.5 to reduce the total area to colonized area. This reduction gives a ratio of planar area of stream surface to substrate area of 2.2, closer to the estimate of 1.60 for Mack Creek.

Drift was collected for 15 minutes every 6 hours in each direction. Duplicate samples were collected with two Miller high speed trawls with 116 micron mesh nets. The samplers were used because their torpedo shape reduced the backwash, a major difficulty with most stream drift samplers. At Oregon State University, samples were weighed while wet

and subdivided. One half was dried in an oven at 50°C for 24 hours, weighed, ashed in a muffle furnace at 500°C for 4 hours, and reweighed. Ash weight was subtracted from oven dry weight to obtain ash-free dry weight. The other half of the sample was soaked for 24 hours in darkness at 4°C in a 90% solution of basic acetone. Fifteen ml of the solution were centrifuged and decanted as previously described. Chlorophyll a concentrations were determined as described and converted to estimates of periphyton biomass. These estimates were adjusted to represent the whole sample by dividing by the percent they represented of the original wet weight of the sample.

Nutrient concentrations in the stream water were determined simultaneously with the operation of the chamber. Samples of the water from the chamber were taken after the closure interval to determine the degree of nutrient depletion or uptake. Nitrate, orthophosphate, total alkalinity, and pH were determined on all samples. Nitrate was determined by the cadmium reduction method (limit of detection - 0.7 µg/l) and orthophosphate was determined by the phosphomolybdate method (limit of detection - 1.0 µg/l) by the Central Chemistry Laboratory, Forest Sciences Laboratory, Corvallis, Oregon. Total alkalinity and pH were measured in conjunction with the measurement of primary production.

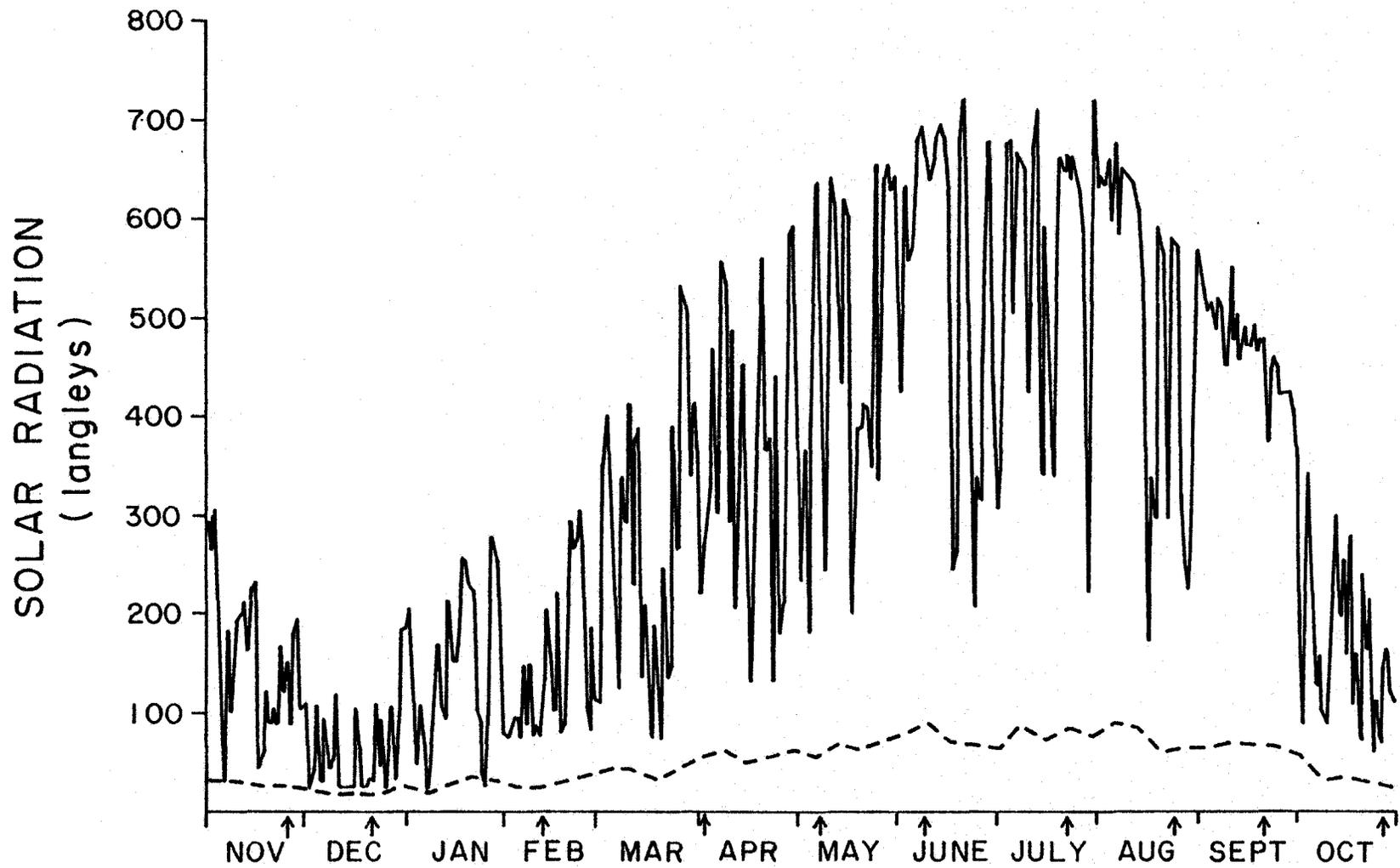
Light intensity was measured with a Belfort pyroheliometer. Stream temperature was measured with a hand-held pocket thermometer. Stream discharge was determined in the culvert between the forest and clearcut sections by measuring current velocity, depth, and width.

Results

Climatic factors exhibited typical patterns for the Pacific Northwest. Both light and stream temperature were maximum during summer months and minimum during winter (Figs. 24 and 25). Precipitation was greatest in the winter and lowest in summer (Fig. 26). Precipitation in late autumn fell mostly as rain and resulted in high streamflows. After late December, precipitation fell mostly as snow and snow depths on the watershed from December through April ranged from 0.5 to 1.5 m. Discharge reflected precipitation patterns, ranging from $3.06 \text{ m}^3 \text{ sec}^{-1}$ (108 cfs) during winter to $0.03 \text{ m}^3 \text{ sec}^{-1}$ (1 cfs) in summer (Fig. 27). Discharge at Lookout Creek gauge station for water year 1975 was 118.3 hm^3 as compared to the 18-year average of 119.0 hm^3 . Therefore, climatic conditions during the study were typical for the west slopes of the Cascade Mountains of Oregon.

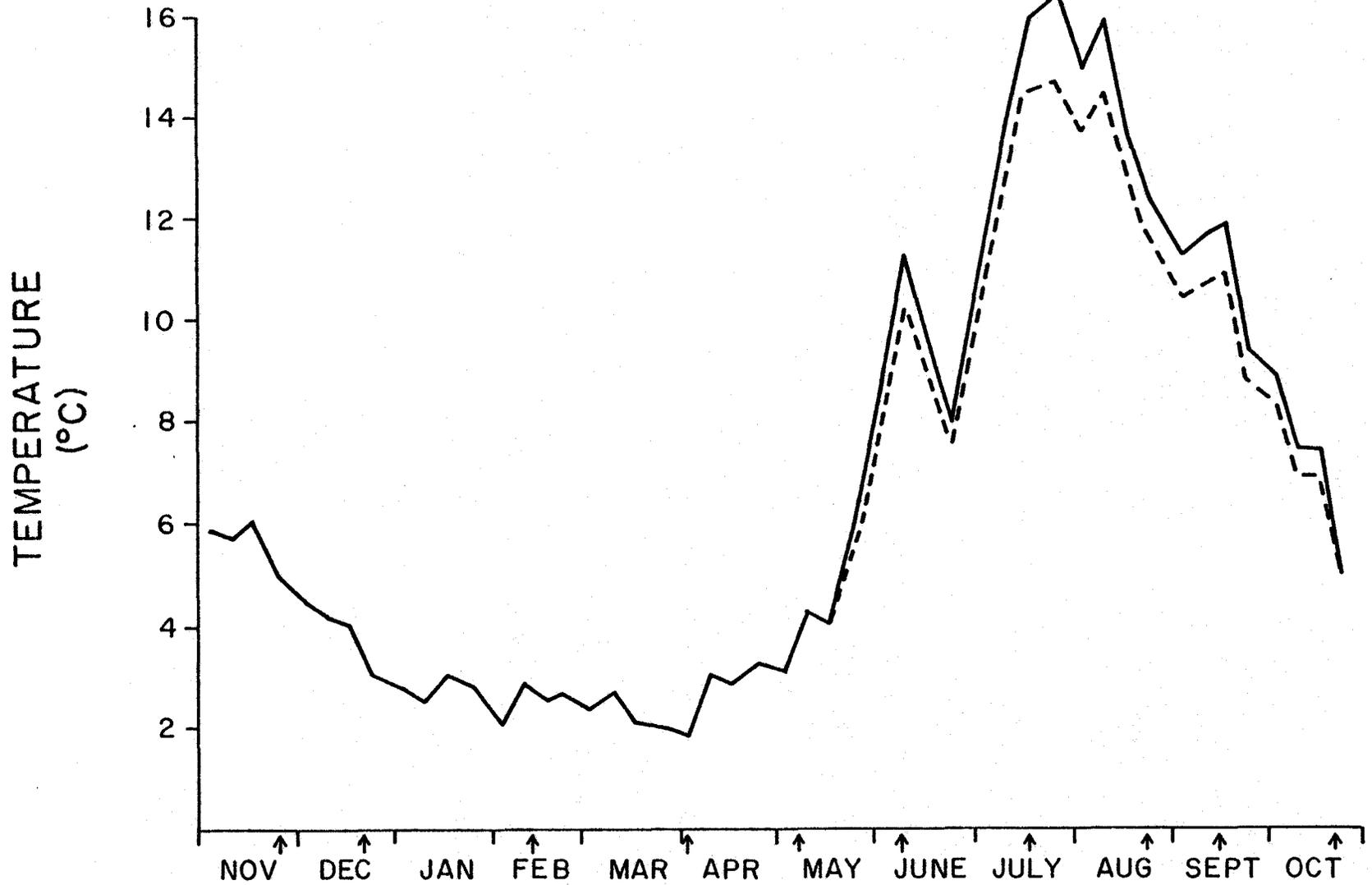
Annual patterns of standing crop of chlorophyll a were not significantly different between the clearcut and forest sections of Mack Creek; however, biomass of primary producers was higher in the clearcut section than in the forested section. Standing crops of chlorophyll a were greater in the clearcut only during the spring months of April and May and the fall months of September and October (Fig. 28). Estimates of standing crop of chlorophyll a in the forested section ranged from a winter low of 8.95 mg m^{-2} to a high of 45.28 mg m^{-2} in early summer. Standing crop of chlorophyll a in the clearcut section was lowest in winter at 11.73 mg m^{-2} and highest in early fall at 43.46 mg m^{-2} . However, periphyton in the forested section had higher B/C ratios than periphyton in the clearcut (Lyford and

Fig. 24. Annual patterns of light intensity in the clearcut and old-growth forest sections of Mack Creek for November 1974 through October 1975. Patterns were calculated from equations relating light intensities at each site to continuous measurements at the meteorological station of the H. J. Andrews Experimental Forest. ($\text{Langleys}_{\text{CC}} = -1.45 + 0.94 \text{Langleys}_{\text{AEF}}$, $r = 0.99$, $n = 8$; $\text{Langleys}_{\text{OG}} = 10.68 + 0.12 \text{Langleys}_{\text{AEF}}$, $r = 0.92$, $n = 9$). Arrows indicate sampling dates. The solid line represents light intensity in the clearcut on a daily basis; the dashed line represents weekly mean light intensities in the old-growth forest.



1975

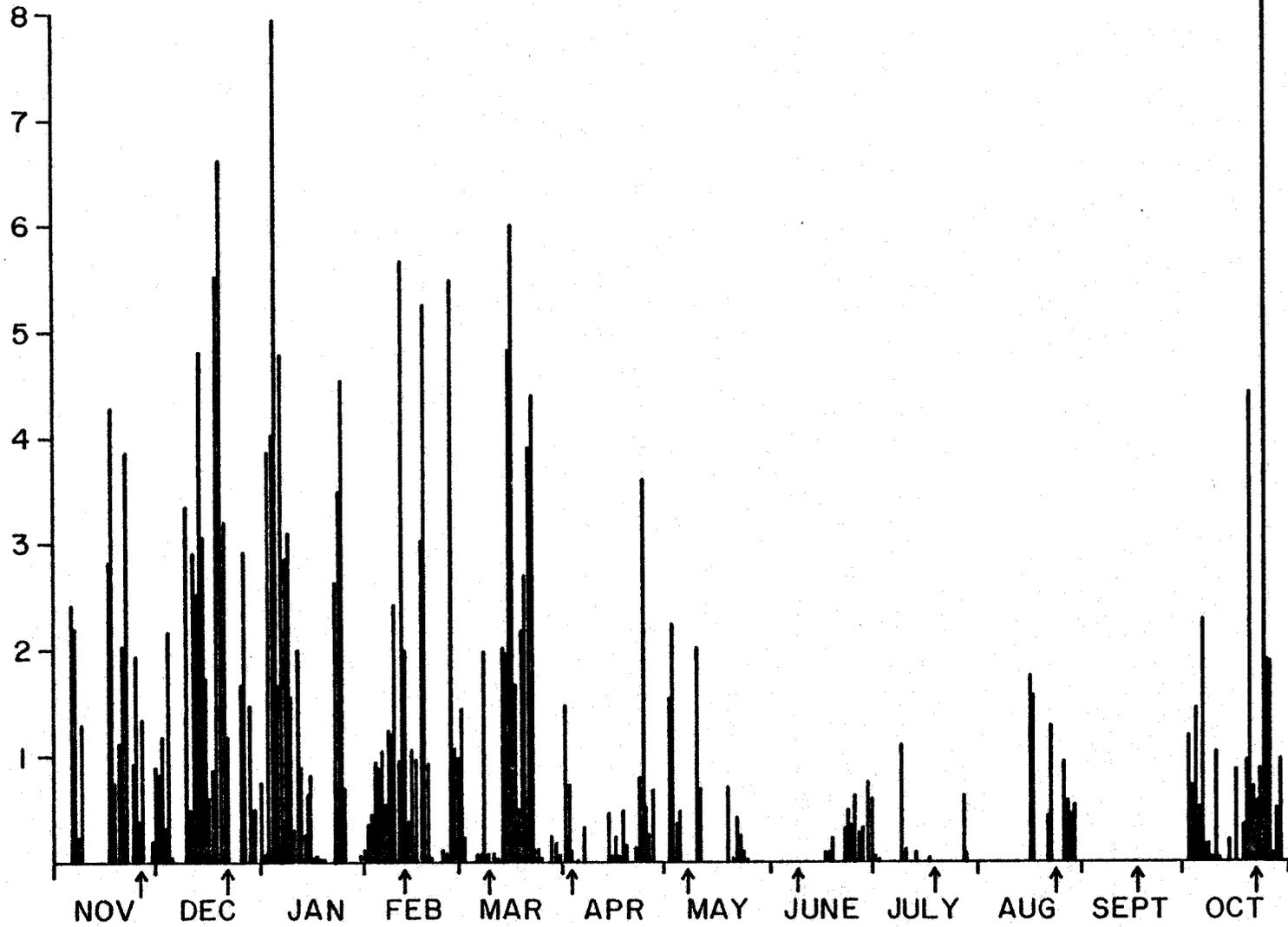
Fig. 25. Annual patterns of stream temperature in the clearcut and old-growth forest sections of Mack Creek for November 1974 through October 1975. Patterns were calculated from equations relating stream temperature at each site to continuous measurements at the Lookout Creek gauging station. Arrows indicate sampling dates. The solid line represents temperature in the clearcut and the dashed line represents temperature in the old-growth forest section.



1975

Fig. 26. Annual pattern of precipitation in the H. J. Andrews Experimental Forest from November 1974 through October 1975. Arrows indicate sampling dates.

PRECIPITATION (cm/day)



1975

Fig. 27. Stream flow in Mack Creek from November 1974 through October 1975. Flow was predicted from an equation developed from data taken at each sampling period and continuous measurements at the Lookout Creek gauging station. Arrows indicate sampling dates.

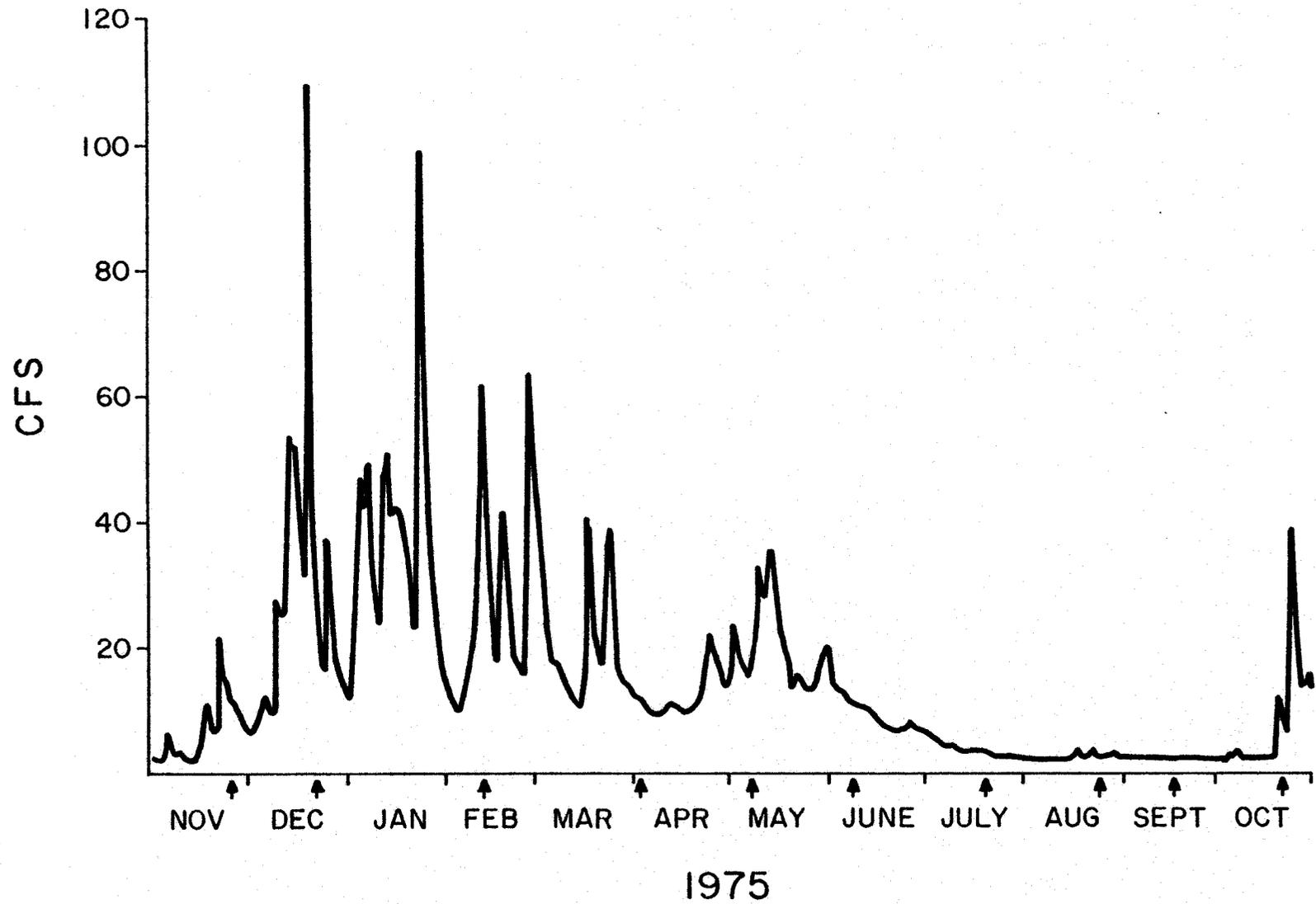
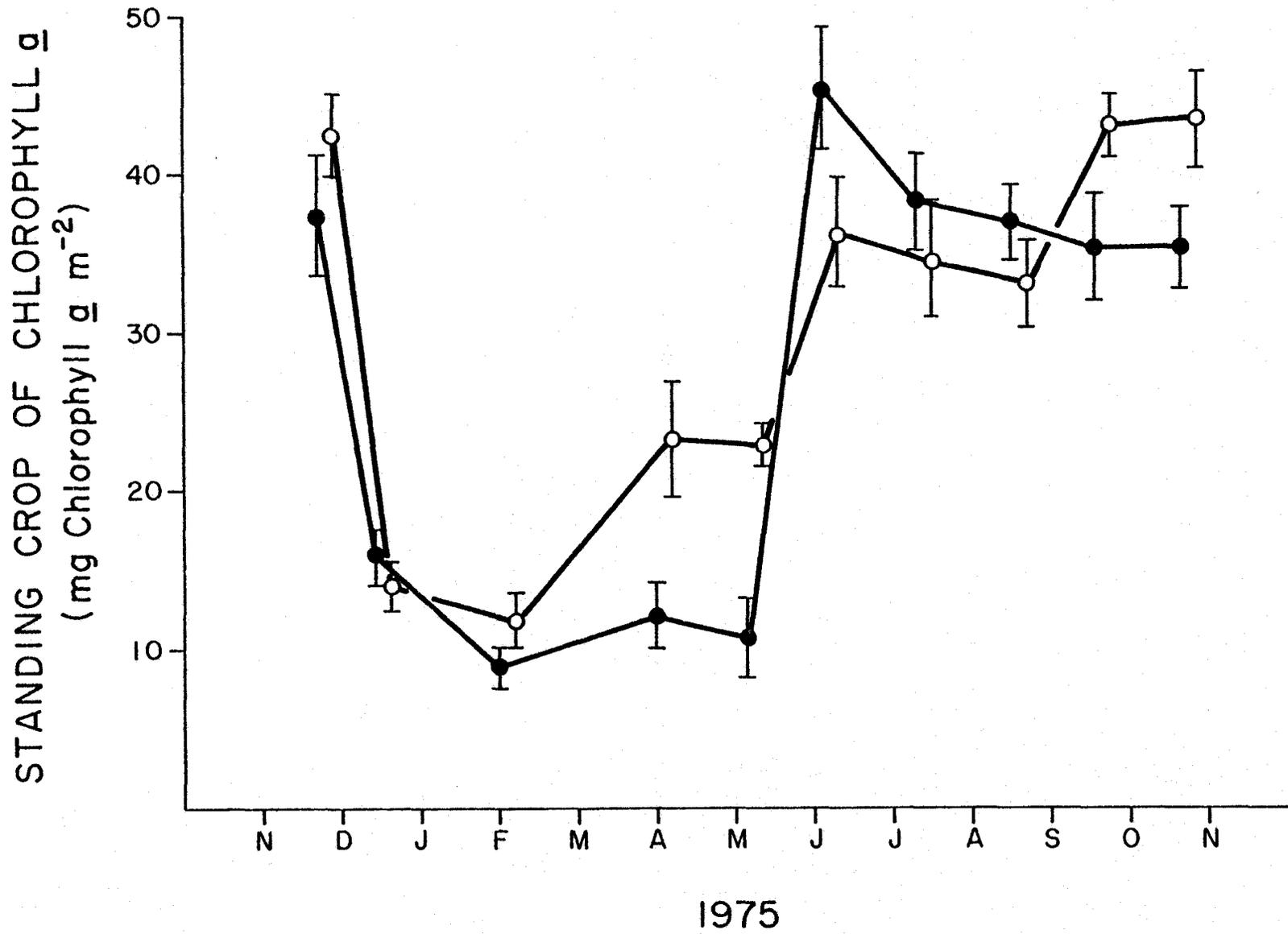


Fig. 28. Standing crops of chlorophyll a in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975. Standing crop is expressed as basis of substrate area and may be converted to planar area by multiplying by 1.60. Points represent means of three samples and bars indicate one standard deviation.



Gregory 1975). Therefore, the greater quantity of periphyton in the clearcut was not reflected in the analysis of standing crop of chlorophyll a. After adjustment for the B/C ratio, annual patterns of primary producer standing crops were distinctly different. Biomass of periphyton was significantly greater in the clearcut at each sampling date except for the early summer months of June and July (Student's *t* test, $p < 0.05$) (Fig. 29). In the forested section biomass of periphyton ranged from $0.48 \text{ g AFDW m}^{-2}$ to $2.45 \text{ g AFDW m}^{-2}$, but the range of biomasses in the clearcut was $0.88 \text{ g AFDW m}^{-2}$ to $3.26 \text{ g AFDW m}^{-2}$.

Rates of gross primary production were greater in the open section of Mack Creek than in the forested section throughout the year (Fig. 30). Gross primary production in the clearcut was greatest in early summer at $136.10 \text{ mg C m}^{-2} \text{ day}^{-1}$ and lowest in winter at $50.15 \text{ mg C m}^{-2} \text{ day}^{-1}$; however, gross primary production in the forested section was substantially lower with a maximum of $73.19 \text{ mg C m}^{-2} \text{ day}^{-1}$ in late spring and $6.75 \text{ mg C m}^{-2} \text{ day}^{-1}$ in winter. Gross primary production in the clearcut for water year 1975 was significantly greater than that in the forested section (randomization test for matched pairs, $p < 0.01$).

The annual pattern of net community primary production was similar to that of gross primary production (Fig. 31). Net community primary production in the clearcut was greatest during early summer at $88.21 \text{ mg C m}^{-2} \text{ day}^{-1}$ and lowest in the fall at $27.93 \text{ mg C m}^{-2} \text{ day}^{-1}$. In the forested section, net community primary production was lower than in the clearcut; production was greatest in late spring at $46.69 \text{ mg C m}^{-2} \text{ day}^{-1}$ and lowest in winter at $-1.01 \text{ mg C m}^{-2} \text{ day}^{-1}$. Net community

Fig. 29. Biomass of periphyton in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 (based on substrate area). Points represent means of three samples and bars indicate one standard deviation.

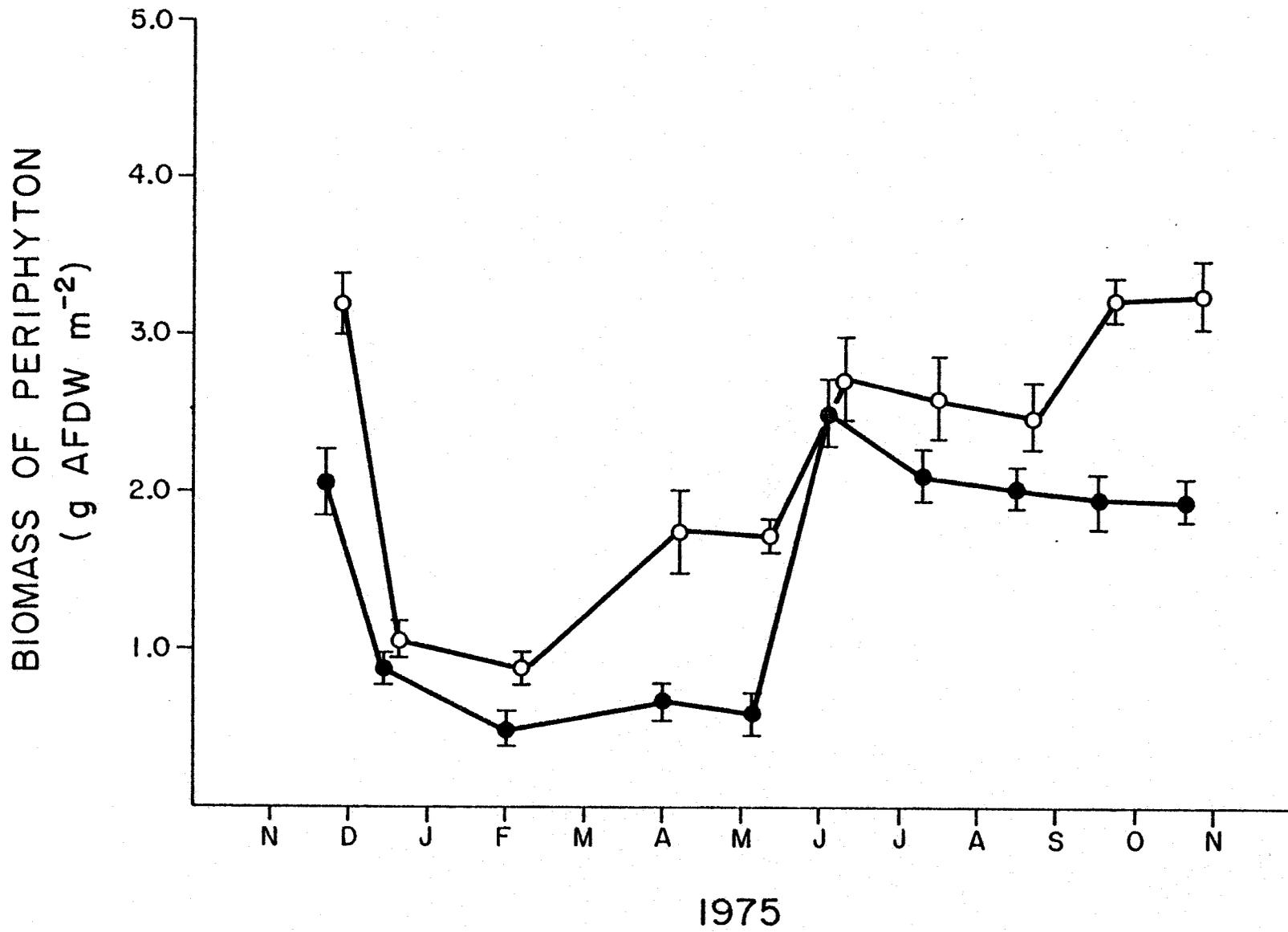


Fig. 30. Rates of gross primary production in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 (based on substrate area).

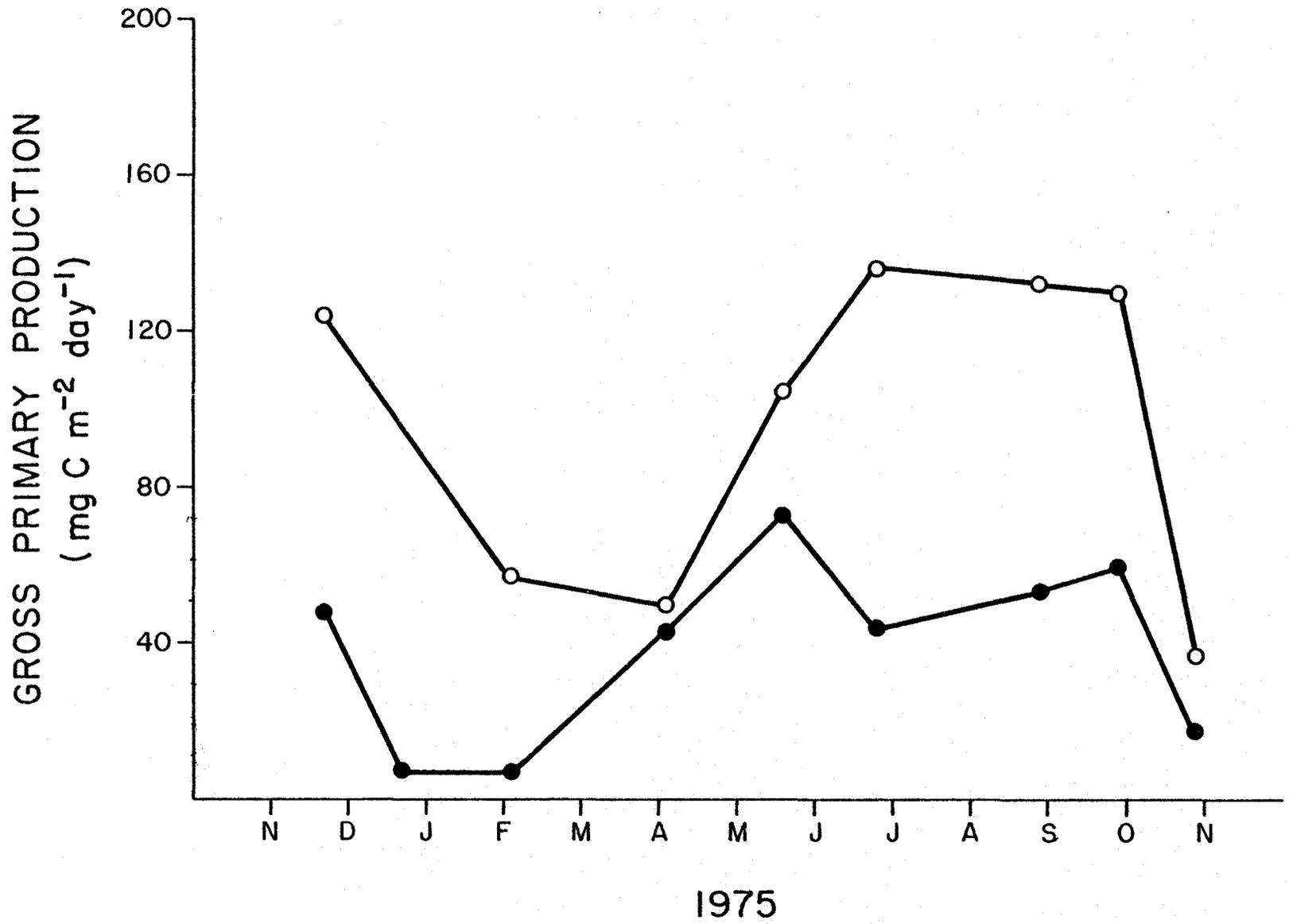
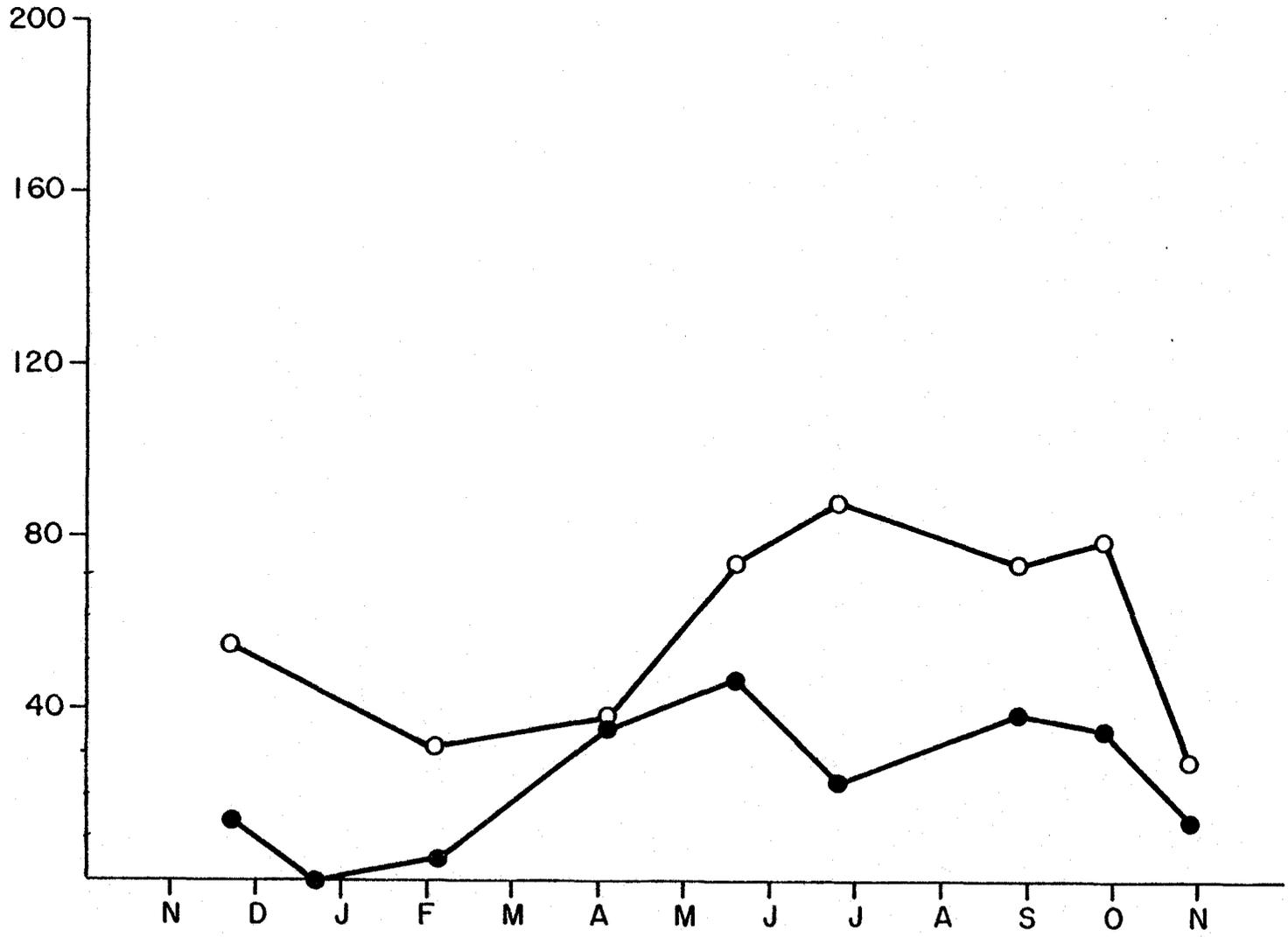


Fig. 31. Rates of net community primary production in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 (based on substrate area).

NET COMMUNITY PRIMARY PRODUCTION

(mg C m⁻² day⁻¹)



1975

primary production was significantly greater in the clearcut than in the forested section for water year 1975 (randomization test for matched pairs, $p < 0.01$).

Community respiration in the two sections of Mack Creek displayed annual patterns similar to primary production (Fig. 32). Community respiration in the clearcut was highest in the fall at $185.71 \text{ mg C m}^{-2} \text{ day}^{-1}$ and lowest in late winter at $29.43 \text{ mg C m}^{-2} \text{ day}^{-1}$. Community respiration in the forested section showed a similar but lower pattern than the clearcut with maximum respiration occurring during fall at $91.40 \text{ mg C m}^{-2} \text{ day}^{-1}$ and minimum respiration occurring during winter at $4.48 \text{ mg C m}^{-2} \text{ day}^{-1}$. Community respiration was significantly greater in the clearcut than in the forested section throughout the year (randomization test for matched pairs, $p < 0.01$).

Annual patterns of P/R ratios showed seasonal maxima and minima similar to those of benthic metabolism (Fig. 33). Ratios were highest in the summer and lowest in the winter. The P/R ratios for the clearcut, however, were not significantly different than ratios observed in the forested section (randomization test for matched pairs, $p < 0.10$). The average annual P/R for the clearcut section was 1.18 and the average P/R ratio for the forested section 1.15. The average P/R ratio for spring and summer (April-September) was significantly greater than the average P/R ratio for fall and winter (October-March) at both sites, 1.60 vs. 0.76 and 1.57 vs. 0.61 for the clearcut and forest, respectively (Mann-Whitney U Test, $p = 0.056$). Therefore, benthic communities on rock substrates in both the clearcut and forested sections were autotrophic in spring and summer, and heterotrophic in

Fig. 32. Rates of community respiration in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 (based on substrate area).

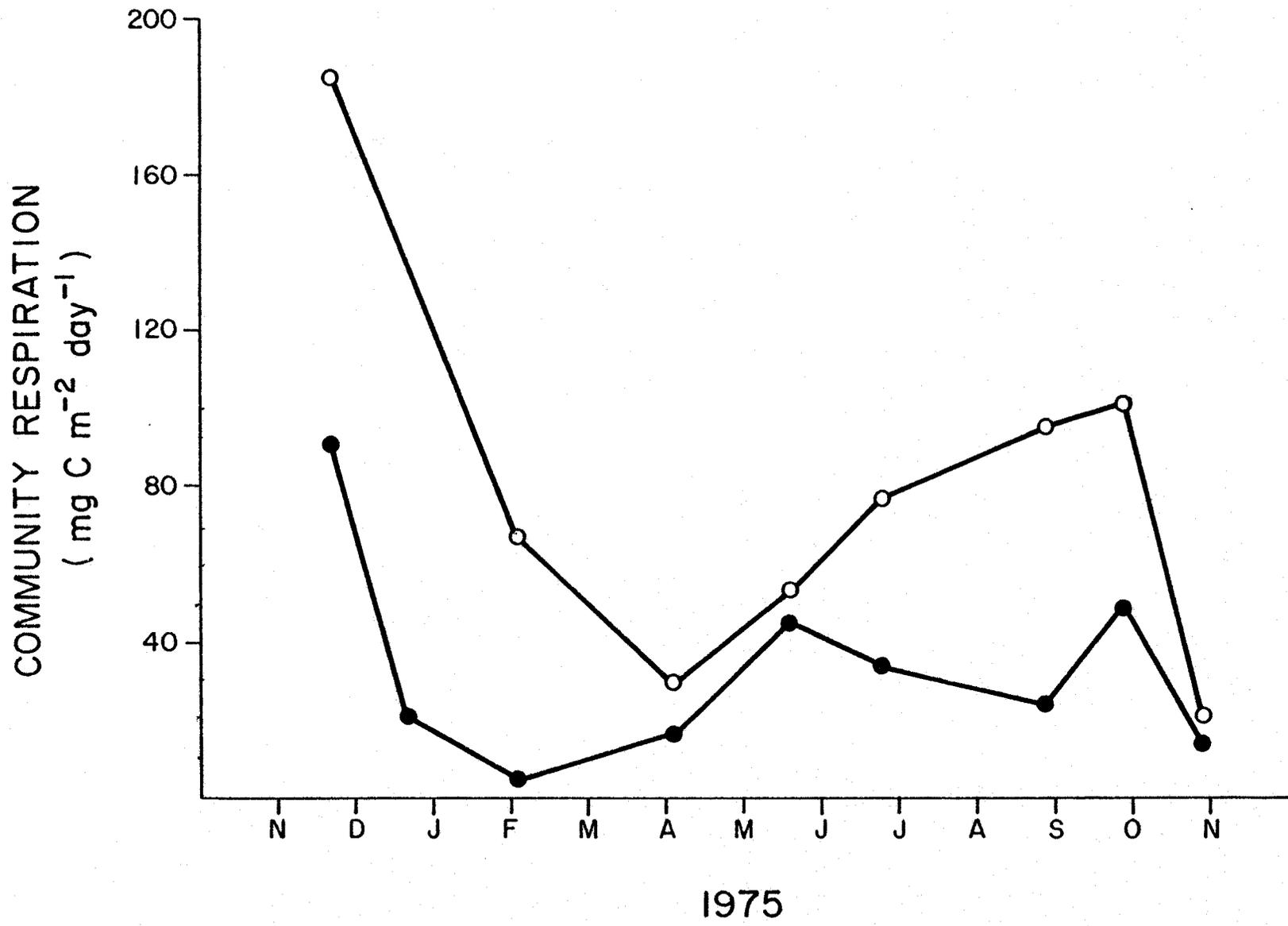
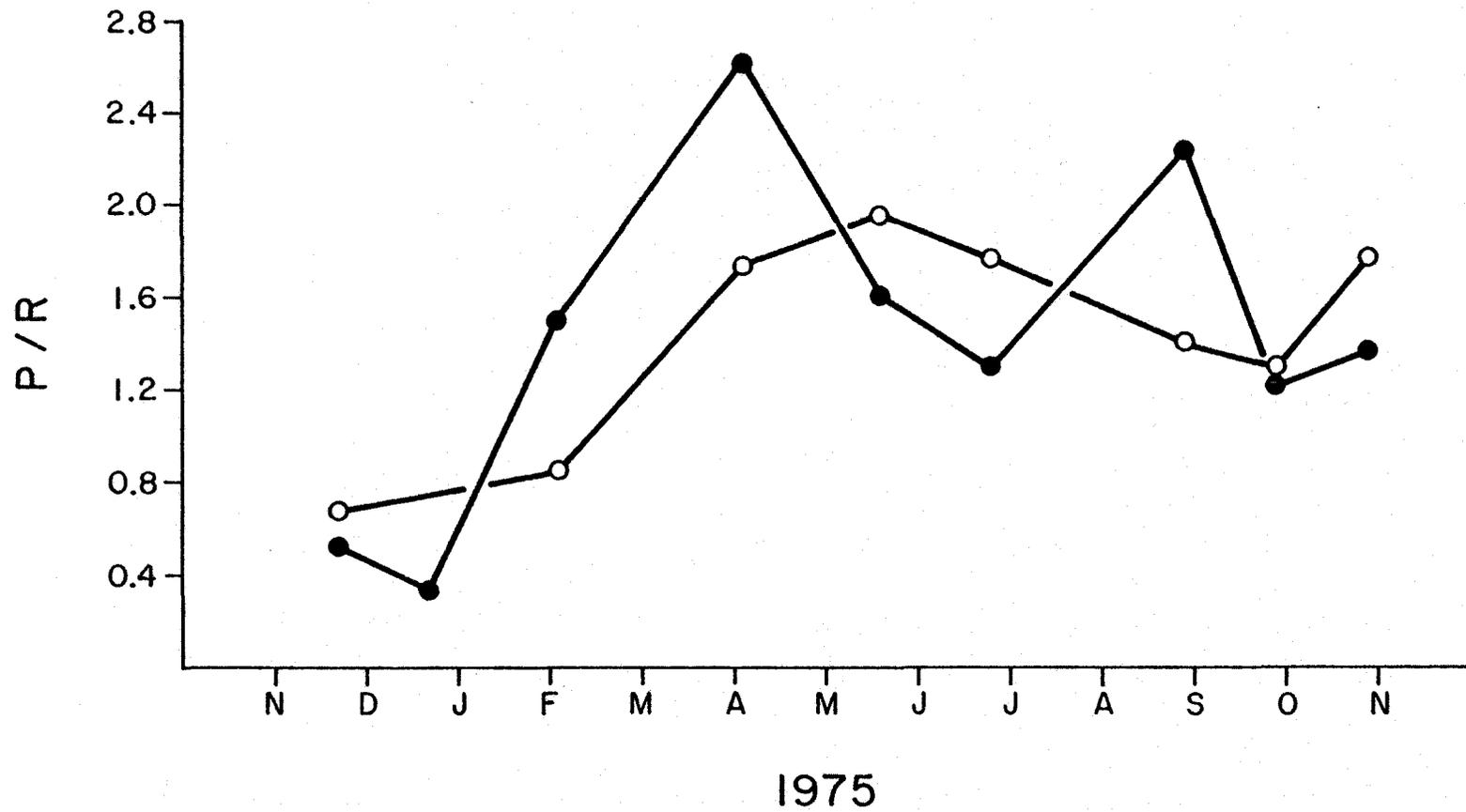


Fig. 33. P/R ratios in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 (P/R = gross primary production/community respiration).



fall and winter, and slightly autotrophic for water year 1975 as a whole.

Patterns and relationships between sites for net daily metabolism were similar to those of P/R ratios (Fig. 34). Net daily metabolism for the open and shaded sections was significantly greater during spring and summer than during fall and winter (Mann-Whitney U Test, $p = 0.018$). Net daily metabolism during spring and summer averaged $43.0 \text{ mg C m}^{-2} \text{ day}^{-1}$ in the clearcut and $19.3 \text{ mg C m}^{-2} \text{ day}^{-1}$ in the forested section. During fall and winter, net daily metabolism averaged $-17.6 \text{ mg C m}^{-2} \text{ day}^{-1}$ in the clearcut and $-10.2 \text{ mg C m}^{-2} \text{ day}^{-1}$ in the forest. Average annual net daily metabolism was $12.7 \text{ mg C m}^{-2} \text{ day}^{-1}$ in the clearcut section and $4.5 \text{ mg C m}^{-2} \text{ day}^{-1}$ in the forested section.

Transport of organic matter in Mack Creek was always greater in the forested section than in the clearcut section except for the June sample. Maximum concentration in transport occurred during late spring and early summer (Fig. 35a). The concentration of organic matter in transport was significantly greater in the forested section than in the clearcut (randomization test for matched pairs, $p < 0.05$). Total transport (concentration multiplied by flow) exhibited two peaks in the forest section and a single peak in the clearcut section (Fig. 35b). The first peak in the forested section was a function of high winter flows. The second peak and the peak in the clearcut came in late spring and early summer, a time of snow melt. Total drift was significantly greater in the forest section than in the clearcut for water year 1975 (randomization test for matched pairs, $p < 0.05$).

Fig. 34. Net daily metabolism in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 based on substrate area.

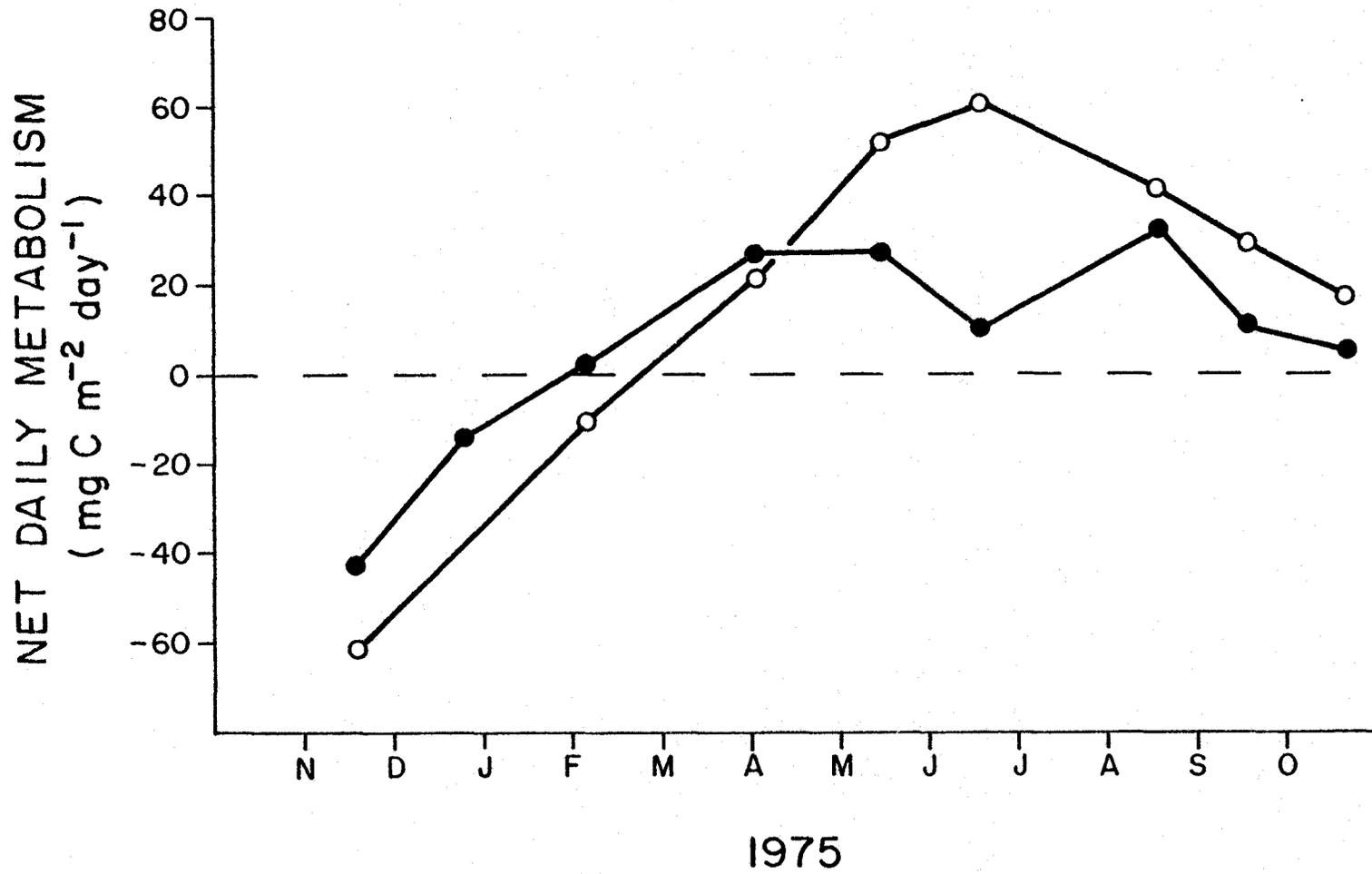
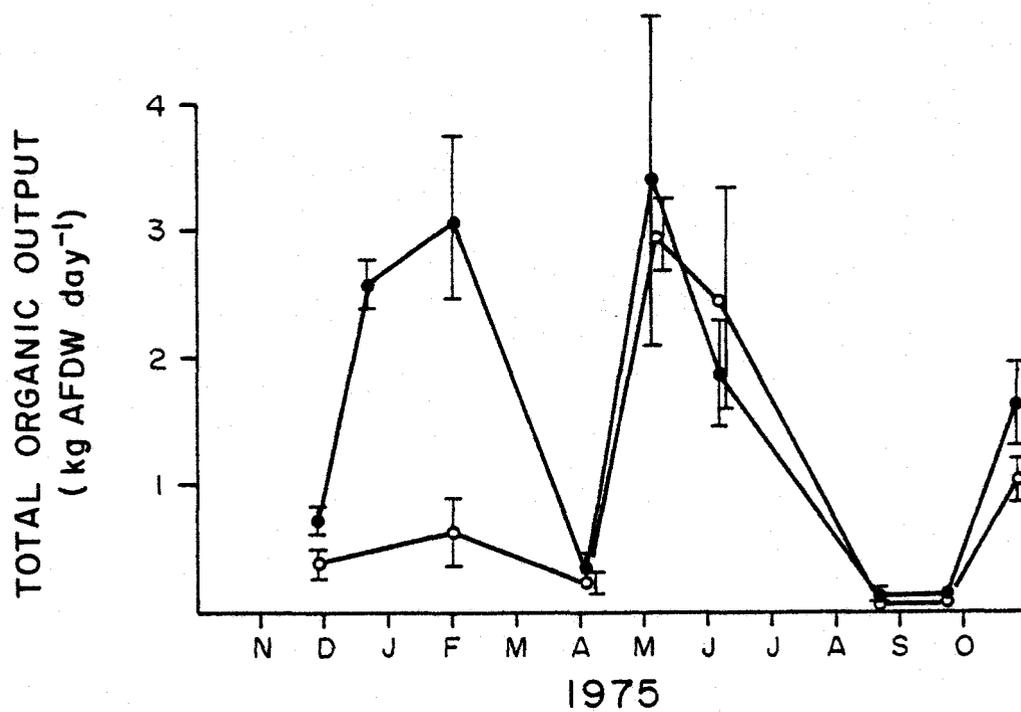
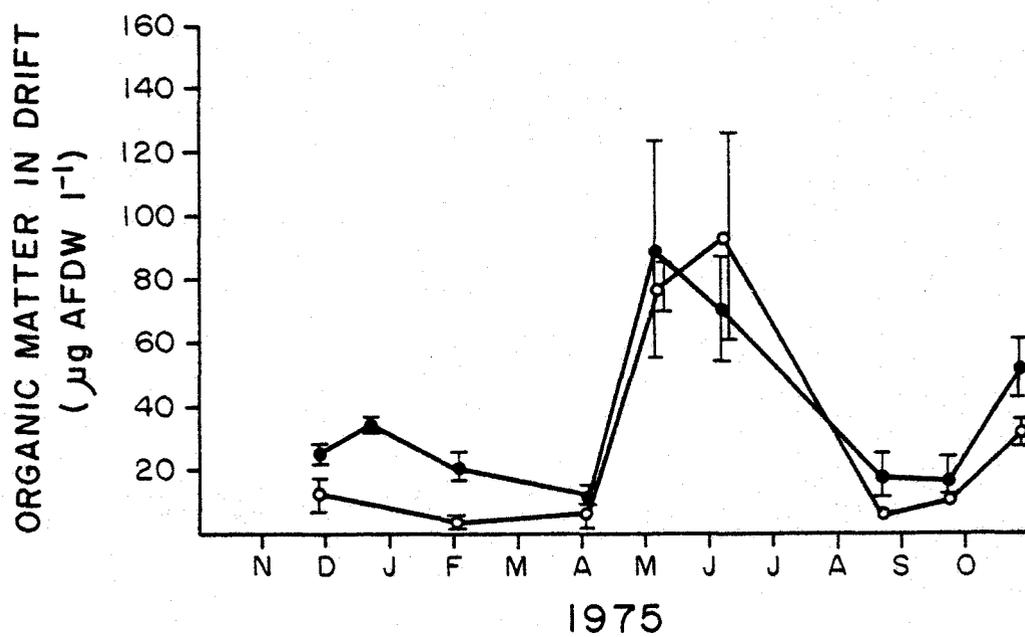


Fig. 35a. Concentration of organic matter in the drift in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 (each point represents the mean of two samples and bars indicate ranges).

Fig. 35b. Total output of organic matter in drift from the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 (each point represents the mean of two samples and bars indicate ranges).



Though transport of organic matter was almost always greater in the forest than in the clearcut, biomass of algae in the drift was always greater in the clearcut. Biomass of algae in the drift showed two major peaks in the clearcut section, one in summer and one fall (Fig. 36a). The amount of algae in the drift in the forest fluctuated but showed no major peaks. The percentage of algae in the drift in the clearcut was more than double that in the forest (Fig. 36b) and was fairly constant, always less than 0.5% in the forest and less than 3.0% in the clearcut. The percentage of algae in the drift was significantly greater in the clearcut than in the forested section (randomization test for matched pairs, $p < 0.05$). However, these observations of drift are representative of base flow conditions; the major transport of organic matter undoubtedly occurs during high flow events. Therefore, these are conservative estimates of annual transport from the forest and clearcut sections, but they do reflect functional differences between the two sites.

Nutrient concentrations in Mack Creek displayed slight variations throughout the year. Nitrate concentrations decreased during summer months in the clearcut section and ranged from 9.9 $\mu\text{g}/\text{l}$ to 41.7 $\mu\text{g}/\text{l}$ (Fig. 37a). Nitrate concentrations in the forest section showed a decrease only in August and ranged from 26.0 $\mu\text{g}/\text{l}$ to 66.0 $\mu\text{g}/\text{l}$. Concentrations of orthophosphate did not display any definite annual patterns at either site (Fig. 37b). Orthophosphate concentrations in the clearcut ranged from 16.6 $\mu\text{g}/\text{l}$ to 79.6 $\mu\text{g}/\text{l}$ and concentrations in the forest ranged from 16.6 $\mu\text{g}/\text{l}$ to 84.0 $\mu\text{g}/\text{l}$. Average annual concentrations of nitrate and orthophosphate in the clearcut were

Fig. 36a. Biomass of algae in the drift from the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 (each point represents the mean of two samples and bars indicate ranges).

Fig. 36b. Percent of drift comprised by algae in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975 (each point represents the mean of two samples and bars indicate ranges).

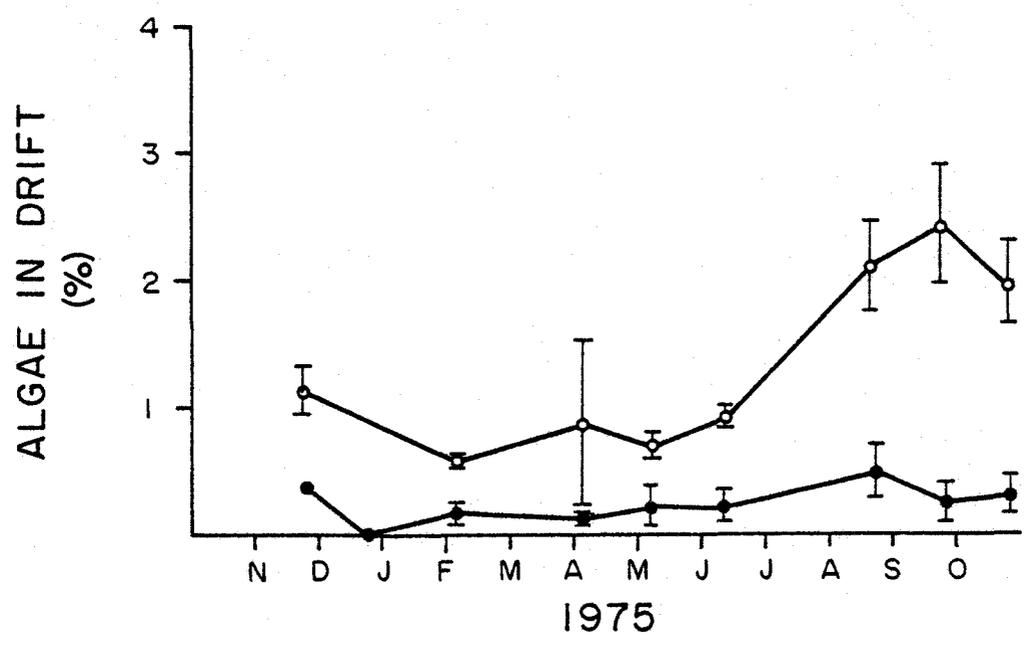
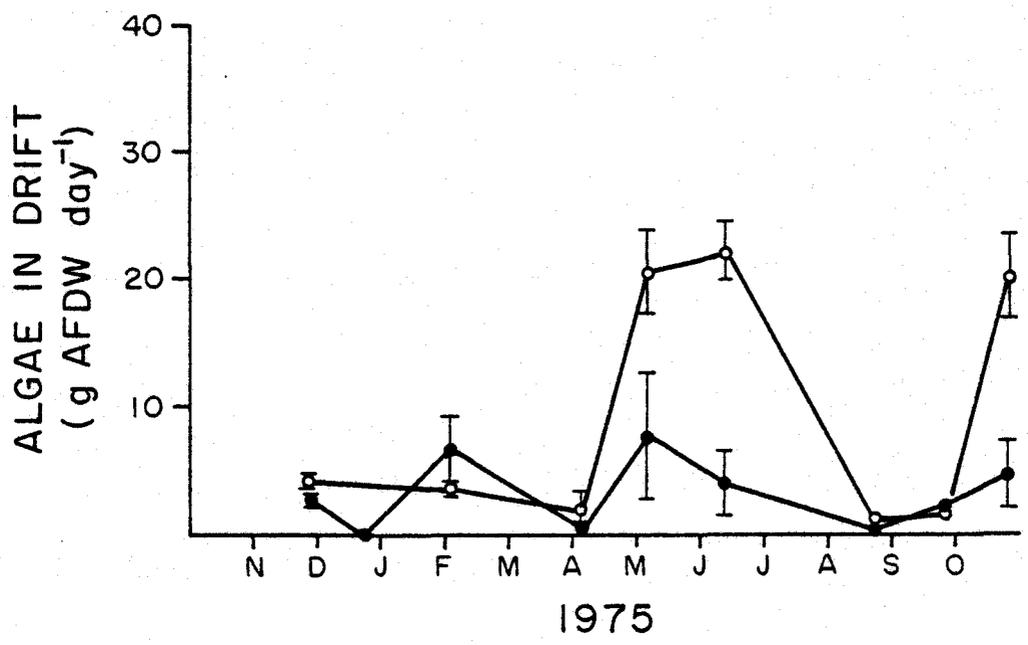
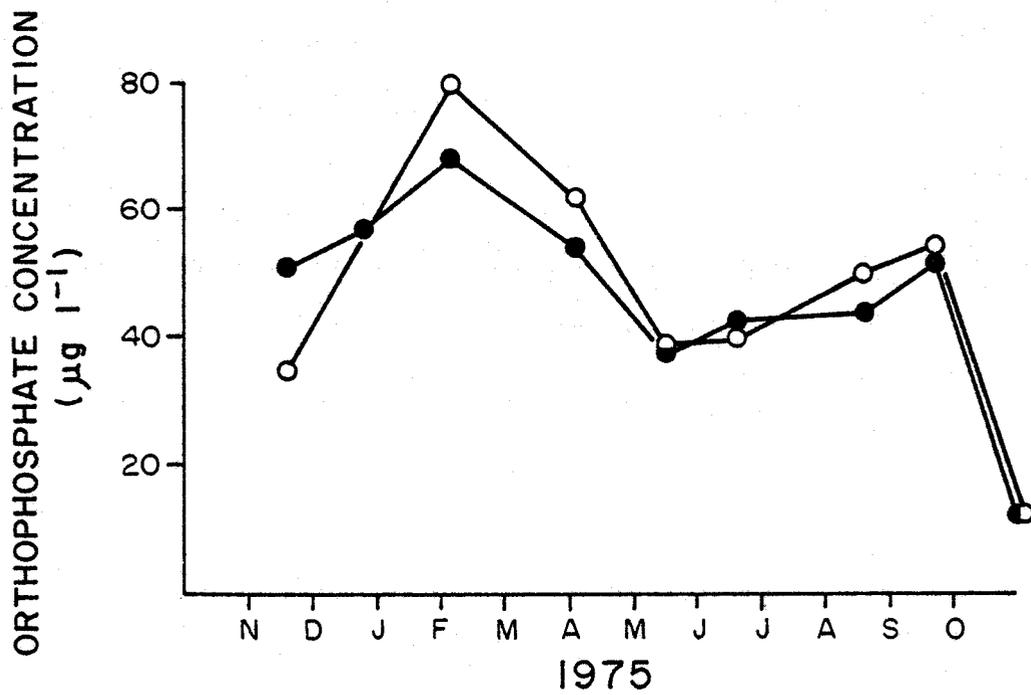
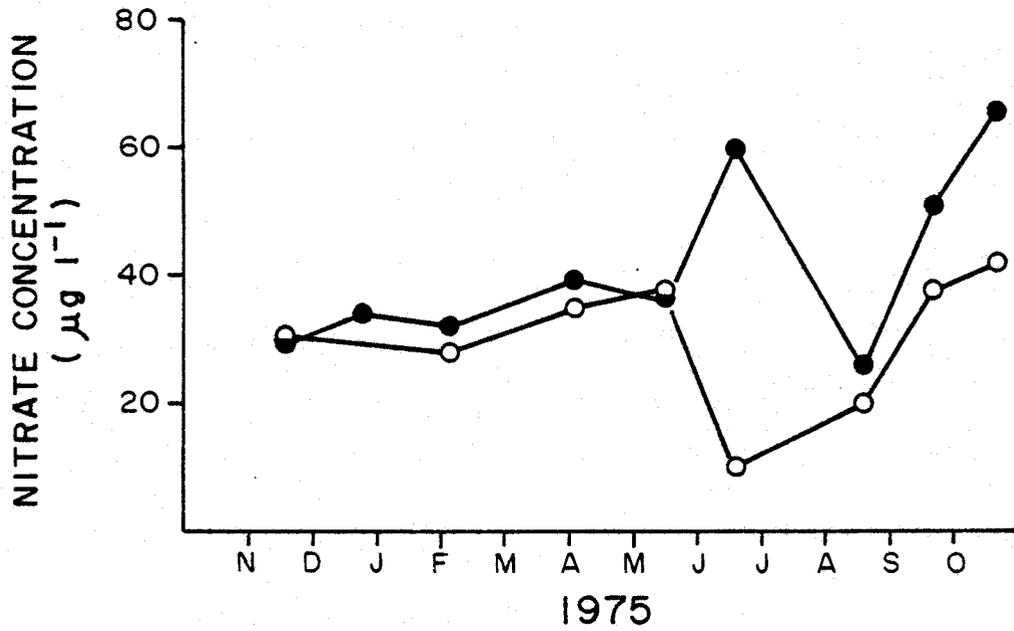


Fig. 37a. Concentrations of nitrate-nitrogen in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975.

Fig. 37b. Concentrations of orthophosphate-phosphorus in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975.

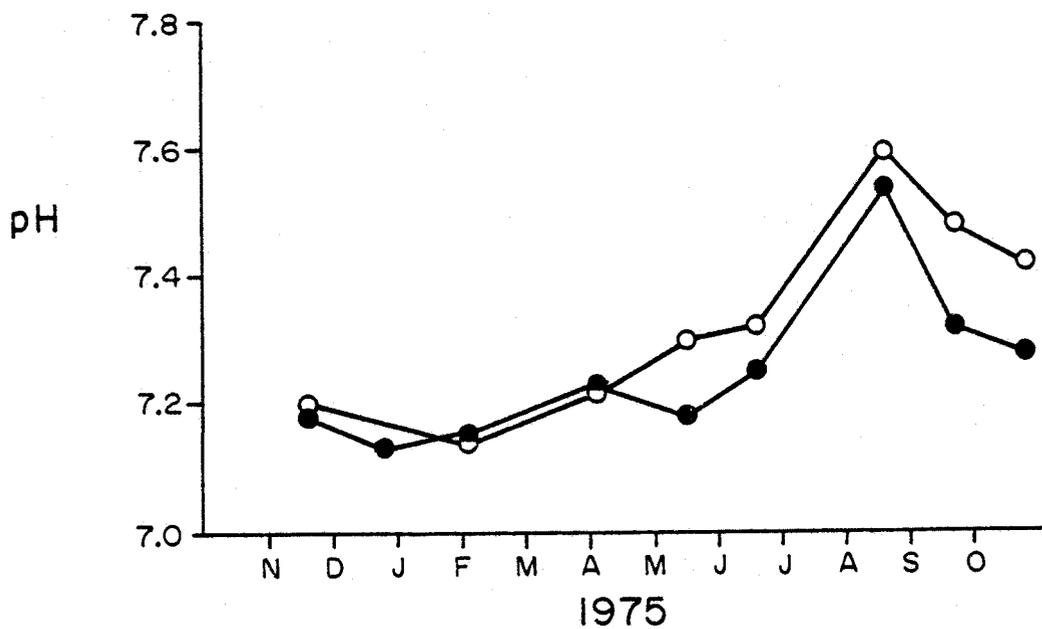
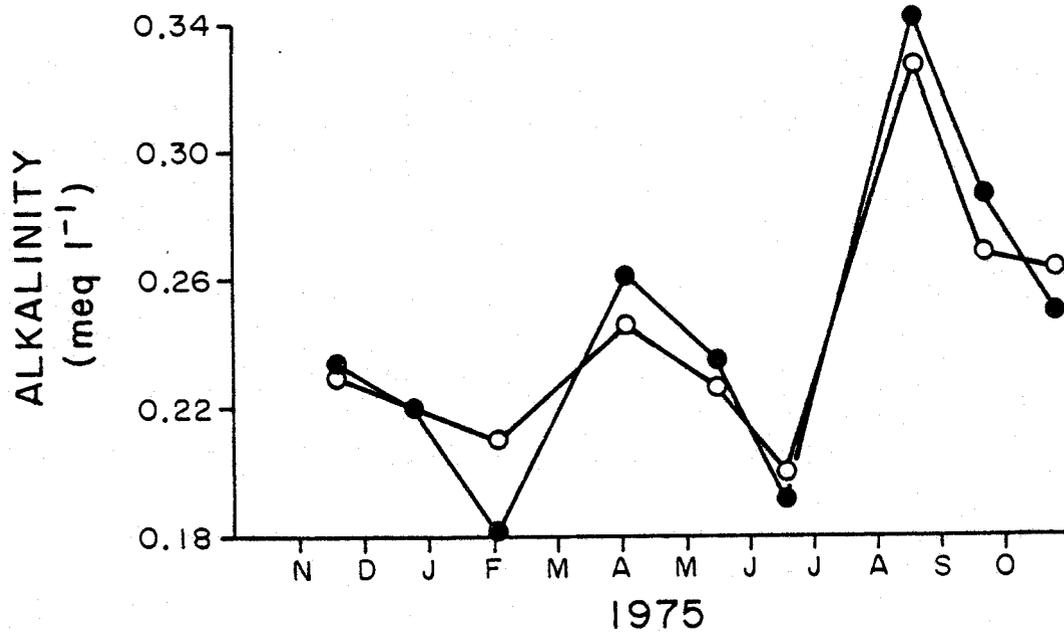


30.3 $\mu\text{g NO}_3\text{-N/l}$ and 48.3 $\mu\text{g PO}_4\text{-P/l}$ and the average annual N/P ratio was 0.82. In the forest, average annual concentrations of nitrate and orthophosphate were 48.3 $\mu\text{g NO}_3\text{-N/l}$ and 50.6 $\mu\text{g PO}_4\text{-P/l}$ and the average annual N/P ratio was 1.10. Alkalinity in Mack Creek was typical of drainages in volcanic regions. Alkalinities were lowest during high flow periods in winter and highest during low flow periods of summer (Fig. 38a). Alkalinities in the clearcut ranged from 0.20 meq/l to 0.33 meq/l and 0.18 meq/l to 0.34 meq/l in the forest. The pattern of pH was similar to that of alkalinity with minimum pH's in winter and maximum pH's in summer (Fig. 38b). In the clearcut, pH ranged from 7.14 to 7.59 and in the forest the annual range was 7.13 to 7.54.

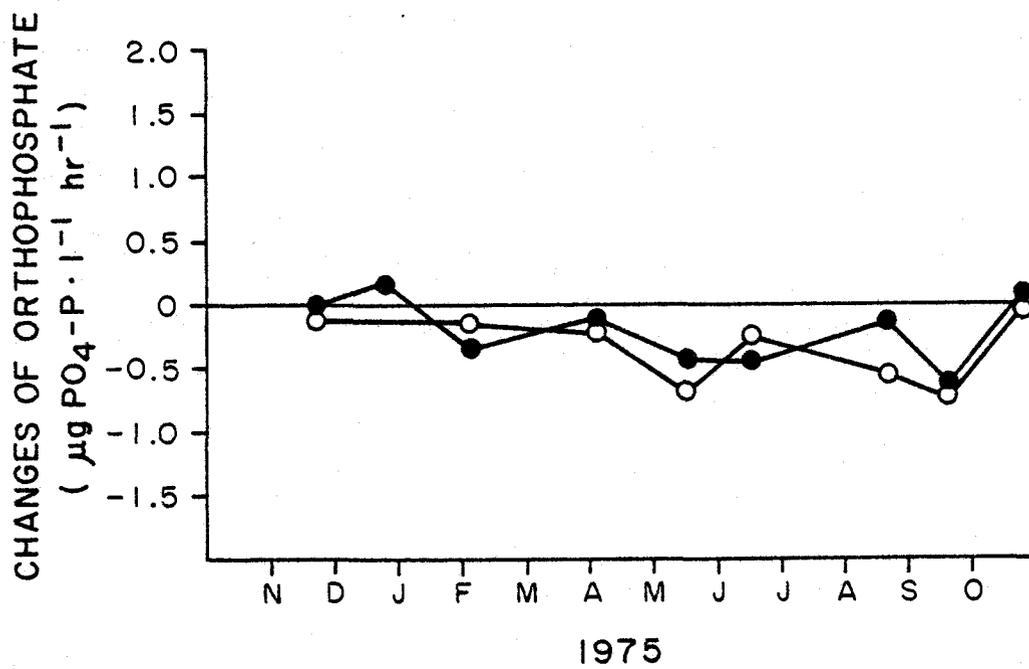
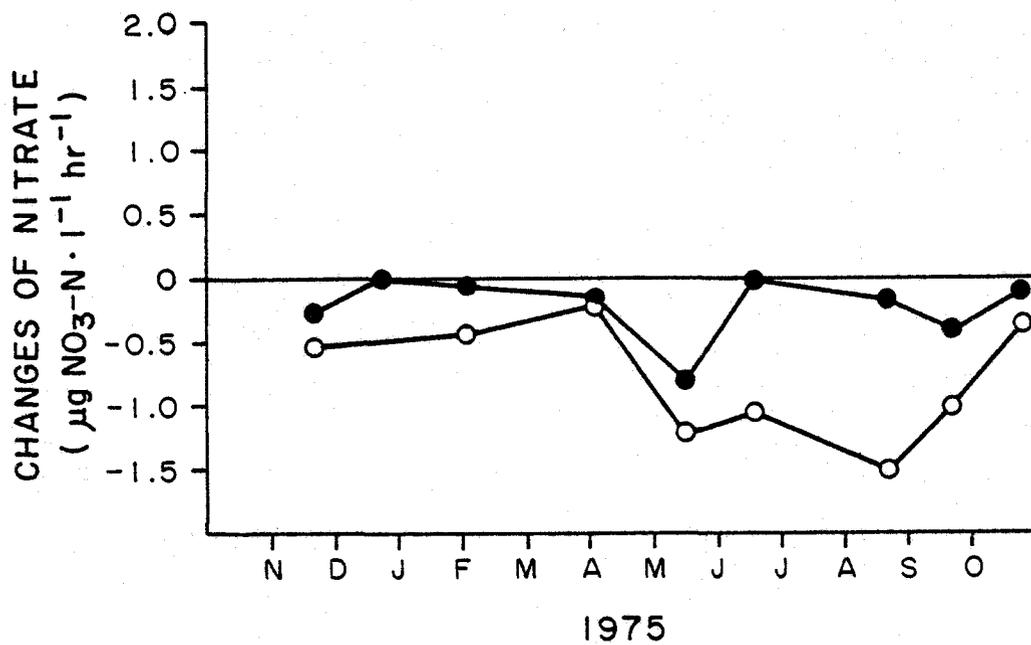
Changes in nutrient concentrations in the chambers demonstrated a greater potential for uptake of nitrate than for uptake of orthophosphate. Uptake of nitrate was observed in the chamber in the clearcut during spring, summer, and early fall (Fig. 39a). Within the forested section, nitrate concentrations in the chamber decreased appreciably only during the May sample. Reductions of orthophosphate were observed in the chamber in the clearcut during summer and early fall, but these reductions were less than the changes in nitrate concentration (Fig. 39b). The nutrient changes in the chambers demonstrated that demand for nitrate exceeded supply and resulted in reductions of available nitrate; however, changes in orthophosphate in the chambers were not as great as for nitrate and not as common. Therefore, the potential for nitrate to limit primary production in Mack Creek was greater than for orthophosphate.

Fig. 38a. Alkalinity in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975.

Fig. 38b. pH in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975.



- Fig. 39a. Rates of change of nitrate in the chamber in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975.
- Fig. 39b. Rates of change of orthophosphate in the chamber in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975.



Productivity of periphyton communities was greater in the clearcut than in the forest. Assimilation number (gross primary production/unit weight of chlorophyll) was greater in the clearcut than in the forested section at all sampling dates except for the months of April and May (Fig. 40). The amount of community respiration per unit weight of chlorophyll a was also greater in the clearcut than in the forested section at all dates except for April and May (Fig. 41). The amount of time required to replace the standing crop of biomass (turnover time) was shorter in the clearcut than in the forest at all times except for April and May. Turnover time based on net community primary production (biomass/NCPP) ranged from 11.7 days to 59.2 days in the clearcut and from 4.5 to 74.6 days in the forest (Fig. 42). Average annual turnover time was 20.5 days in the clearcut section and 21.4 days in the forest. Turnover times in the two sites on Mack Creek were not significantly different; also, there were no significant seasonal differences in turnover times at either site (Wilcoxon matched-pairs signed ranks test, $p < 0.05$).

Efficiency of light utilization was greater in the shaded section of Mack Creek than in the open section; photosynthetic efficiencies were low, in general. Photosynthetic efficiency expresses the ability of primary producers to utilize the energy of incident light; it is the total production of calories of organic matter per calorie of light. Efficiencies in the forested section ranged from 0.11% to 0.81% and in the clearcut they ranged from 0.03% to 0.22% (Fig. 43). Efficiency of primary production was greater in the forested section at all times except for the February sample; this difference was

Fig. 40. Assimilation number (based on chlorophyll a) in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975.

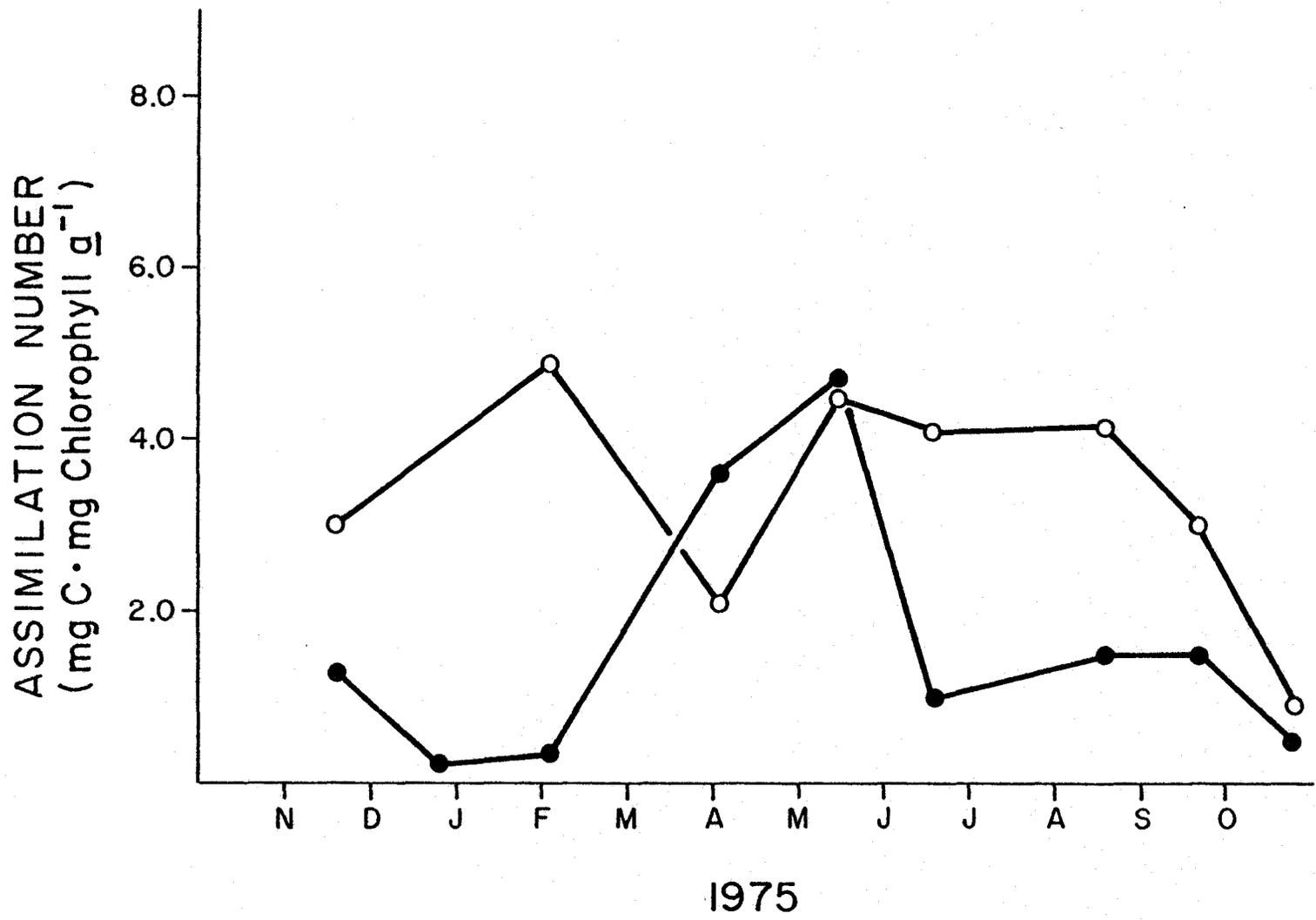


Fig. 41. Community respiration per unit chlorophyll a in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975.

COMMUNITY RESPIRATION / UNIT CHLOROPHYLL
(mg C · mg Chlorophyll⁻¹ · g)

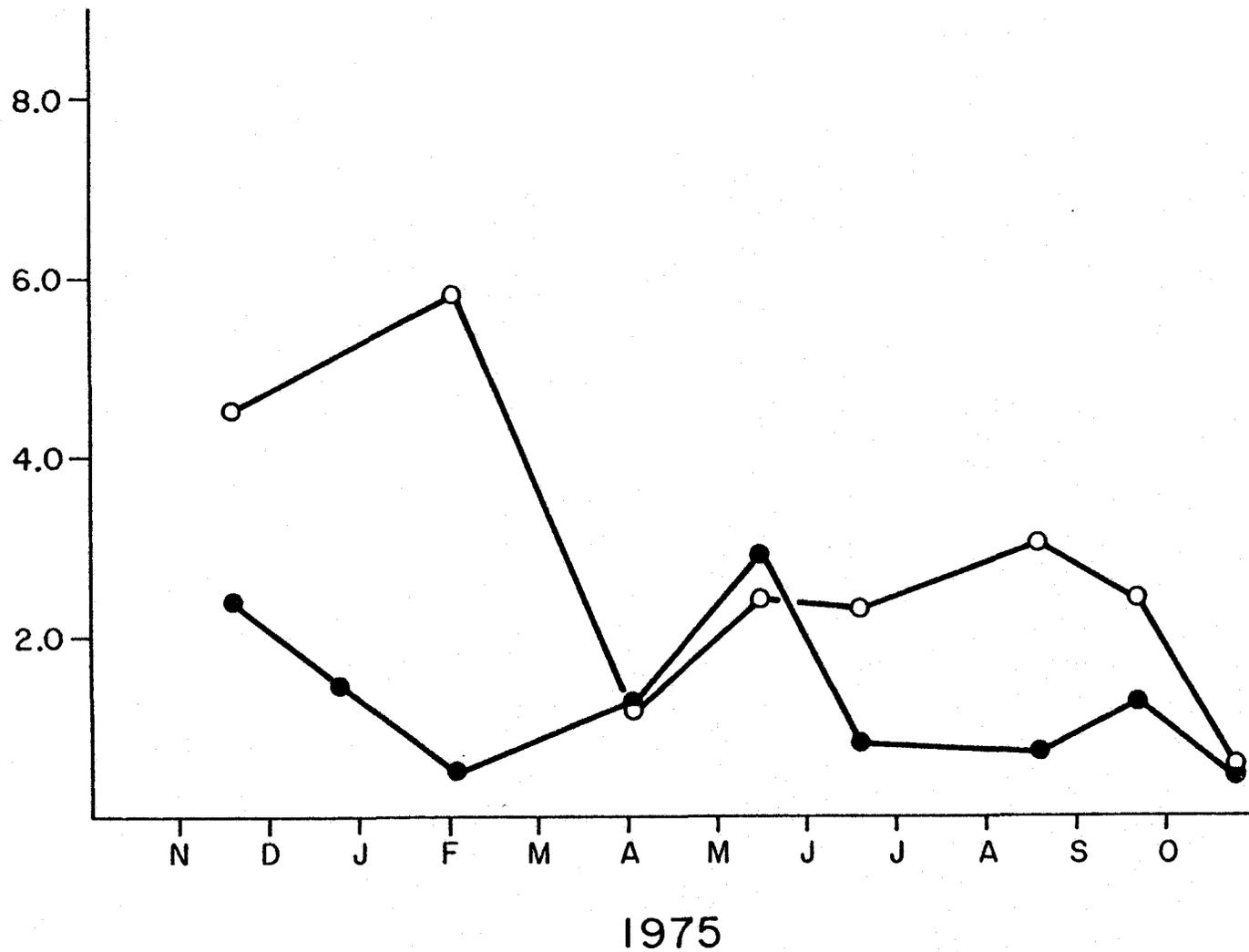


Fig. 42. Turnover time (based on net community primary production) in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 and October 1975.

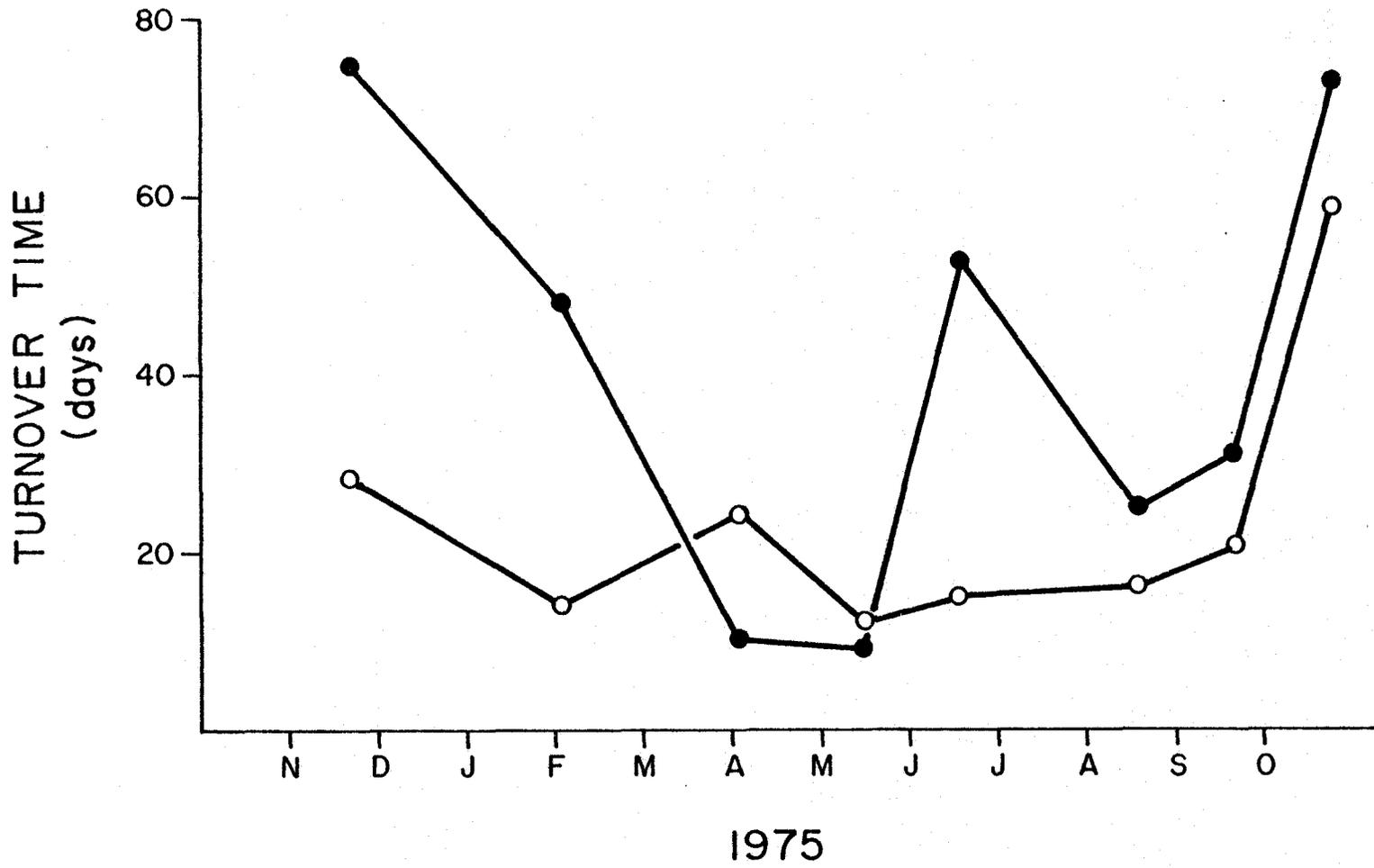
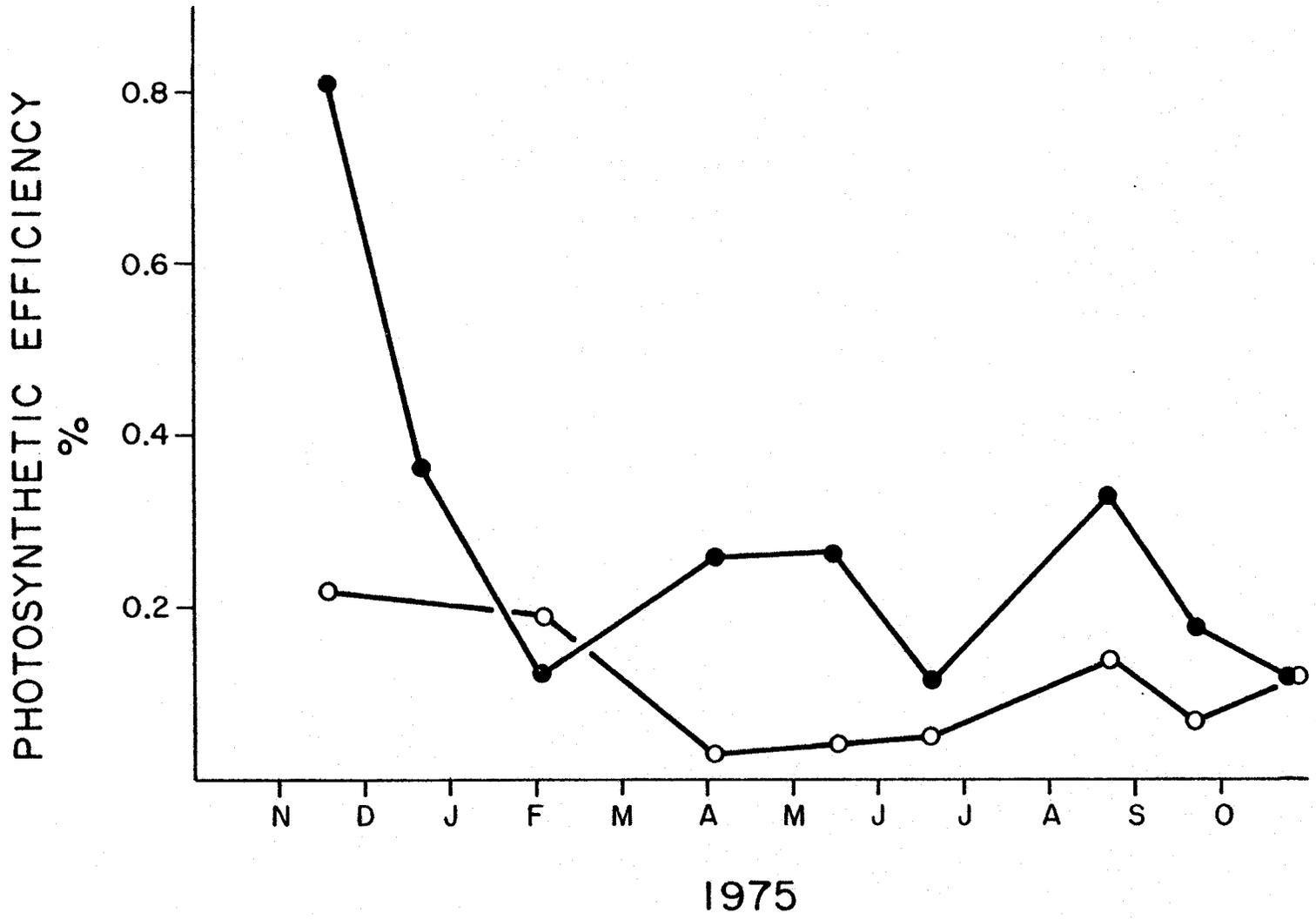


Fig. 43. Photosynthetic efficiency in the clearcut (O) and old-growth forest (●) sections of Mack Creek from November 1974 through October 1975.



statistically significant (Wilcoxon matched-pairs signed-ranks test, $p < 0.05$). Efficiencies were significantly greater in the summer than during winter in the clearcut section (Mann-Whitney U test, $p = 0.036$). No significant seasonal trend in photosynthetic efficiencies in the forested section was found. The low efficiencies observed in Mack Creek were reflective of the low productivity of the system.

Discussion

Primary producer processes in Mack Creek were greatly enhanced in the clearcut as compared to the old-growth forest section. Though many factors may influence primary production, higher light intensities were the major cause of increased primary production in the open site. Therefore, clearcutting created an open rather than a shaded stream and enhanced the contribution of autochthonous primary production to the energy base of Mack Creek.

Only two previous studies have examined the effects of clearcutting on primary production and standing crops of periphyton in streams. Rates of primary production and standing crops of periphyton were measured in Needle Branch, a stream in the Coast Range of Oregon for 18 months prior to logging and 18 months after logging (Hansmann 1969). The same measurements were also made in a forested stream in an adjacent watershed (Flynn Creek) during the same period. Standing crops of chlorophyll in Needle Branch were lower after logging than before and were also lower than those in Flynn Creek at the same time. These results were opposite the response observed in Mack Creek; this may be partly explained by the fact that Hansmann's study was conducted

immediately after logging. Sedimentation and channel instability may have been responsible for the reduced standing crops. Rates of primary production in Needle Branch after logging were the same as rates observed prior to logging and greater than rates of production in Flynn Creek at the same time. Therefore, primary production per unit weight of periphyton was greater in Needle Branch after logging, a relationship that was also observed in Mack Creek. Another study examined the effects of clearcutting on primary producers in a stream in a 5 year old clearcut, Ritherdon Creek, and a stream in an old-growth forest, Carnation Creek, on Vancouver Island, British Columbia (Stockner and Shortreed 1976). Standing crops of chlorophyll a and biomass of periphyton was slightly lower in the forested site. Though rates of primary production were not measured directly, accumulation of algae was determined to provide an approximation of net production. Rates of colonization were slightly greater in Ritherdon Creek than in Carnation Creek. The authors attributed the slight response to nutrient limitation. The responses of primary producers in Ritherdon Creek and Carnation Creek were similar to those observed in Mack Creek but much lower. Removal of terrestrial vegetation by clearcutting exposes streams to greater inputs of solar radiation and increases the potential for primary production. Enhancement of primary producers may be masked, however, by initial detrimental effects such as sedimentation, substrate instability, or high temperatures.

Standing crops of primary producers and rates of primary production under open and shaded conditions have shown similar responses to periphyton in logged and unlogged areas. Numbers of

algal cells per unit area in a section of Berry Creek, Oregon, that had been opened by removal of streamside trees were greater in summer than in an adjacent reach that was forested (Dever 1962). In open and shaded artificial channels at Kalama Springs, Washington (a research facility of the Weyerhaeuser Company), standing crops of periphyton and rates of primary production were greater in open channels (Busch 1978). A number of field and laboratory studies have demonstrated that light regulated primary production in streams (Lane 1965, McIntire and Phinney 1965, Tominga and Ichimura 1966, Hall 1972, Kelly et al. 1974, Naiman and Gerking 1975, Pfeifer et al. 1975, Hornberger et al. 1976, Gallegos 1977, Sumner and Fisher 1979). Factors that influence the quantity of light available to streams may play a major role in determination of structure and productivity of stream ecosystems.

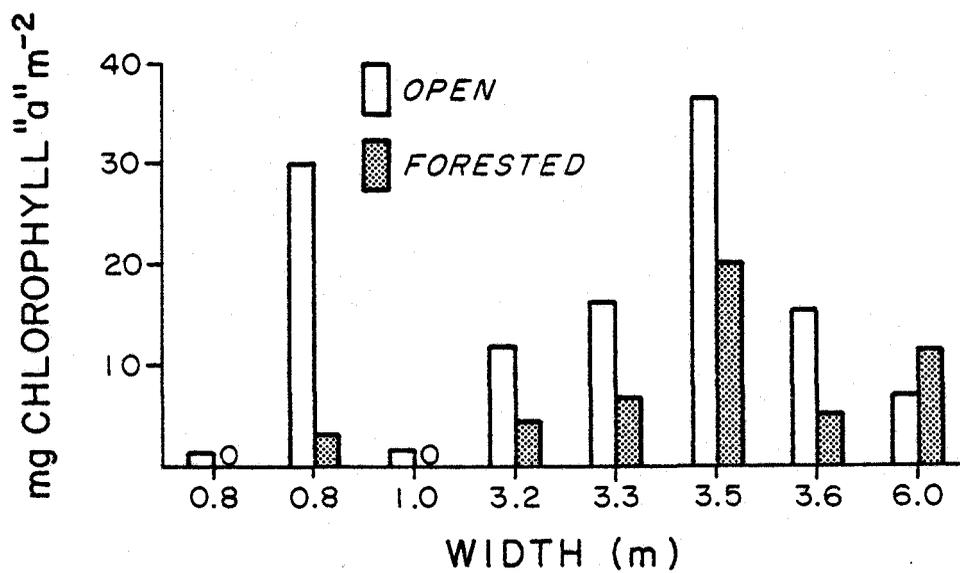
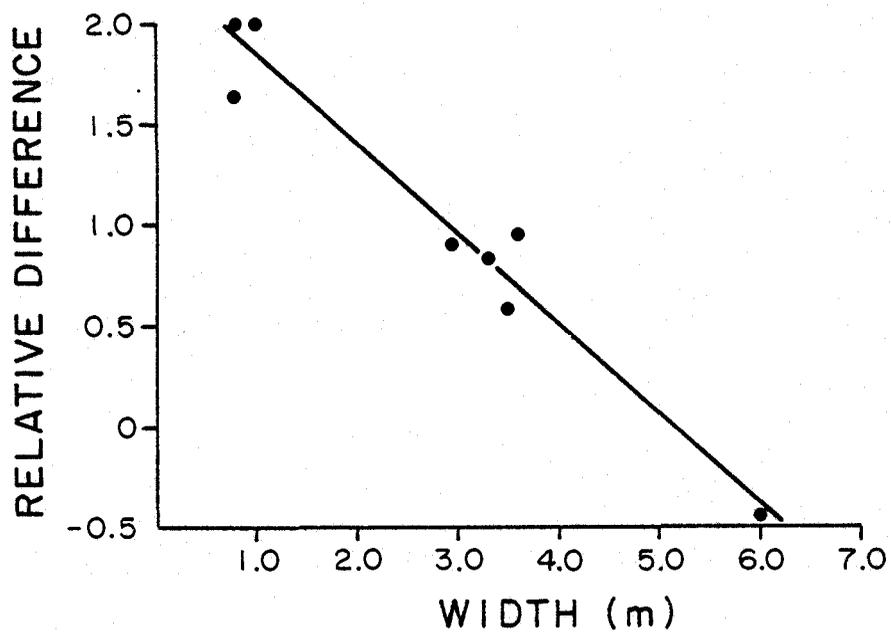
Standing crop and primary production in the open and shaded sites on Mack Creek displayed seasonal patterns with minima in winter and maxima in summer. Decreased primary production in summer has been observed in streams in deciduous forests as a result of shading by the canopy in summer (Hall 1972). There was no decrease in primary production in Mack Creek in summer because the dominant streamside vegetation was coniferous. However, the distinct pattern of solar radiation in the Pacific Northwest with full sunlight in summer and low light levels in winter as a result of heavy cloud cover may play a major role in determining patterns of standing crops of periphyton that were observed in my study. Similar seasonal patterns have been observed in other streams in coniferous watersheds (Lane 1965, Hansmann 1969, Stockner and Shortreed 1976).

Cloud cover that causes distinct seasonal patterns in sunlight also results in heavy rainfall and flooding that may scour periphyton and account for the low standing crops in winter. High flows have been observed to increase export of periphyton (Douglas 1958, McIntire 1964, Stockner and Shortreed 1976). Research by James Rounick and this author (manuscript in preparation) examined patterns of periphyton standing crops in streams in the H. J. Andrews Experimental Forest during the winter of 1977, a period of drought in the Pacific Northwest. The first major storm occurred during March as opposed to early fall when winter storms usually begin. Standing crops of periphyton in January and February were as high or higher than in the previous summer. Therefore, scour by winter storms appears to be the major determinant of periphyton standing crops in winter. Low light levels in winter may control the rate of recovery of periphyton after storms.

Increase in potential for primary production as a result of deforestation is a function of the relative change in solar radiation. If a stream was relatively open prior to logging, less response to canopy removal should be observed. In cooperation with Mike Murphy, I examined this relationship in eight pairs of open and forested sites on streams in the H. J. Andrews Experimental Forest and in the surrounding McKenzie River drainage (Murphy 1979). Smooth brick field tiles, 58.2 cm², were placed in each of the sites and allowed to colonize for 4 weeks; at the end of that period, standing crops of chlorophyll a were determined on each of the tiles. Standing crops were higher in the open sections in all of the sites except the largest stream (Fig. 44a). Shading by the forest canopy is a function of stream

Fig. 44a. Standing crops of chlorophyll a after 4 weeks in 8 pairs of clearcut and old-growth sites on streams of different size. Each histogram represents the mean of two samples and bars indicate one standard deviation.

Fig. 44b. Relative differences between colonization in clearcuts as opposed to old-growth sites as a function of stream width.



width. As the stream widens, the canopy opening over the stream widens and allows more light to reach the stream. Relative change in standing crop of periphyton was inversely related to stream width (Fig. 44b). Change in standing crop was most dramatic in smaller streams. The relative response of primary producers to logging will be greatest in low order streams (first- to third-order streams) and no effect may be observed in higher order streams.

Temperature played a minor role in determining the difference in primary production between the clearcut and forested sections of Mack Creek. Observed temperature differences between the sections in the forest and the clearcut were less than 2°C in the summer and no difference was observed in winter. Aho (1976) also found a similar temperature pattern in the two sites in the previous year. In laboratory stream studies, temperature increases of 10°C only increased gross primary production by 30% and had no significant effect on gross primary production at light intensities greater than 11000 lux (Phinney and McIntire 1965). In view of the small differences in temperature observed between the two sites, it must be concluded that temperature had little influence in the response of primary producers to clearcutting in Mack Creek.

Photosynthetic efficiencies in Mack Creek were low but well within the range observed in other aquatic systems. The range of photosynthetic efficiency in Mack Creek was 0.03% to 0.81%. Tilzer et al. (1975) reviewed efficiency of light utilization by lake phytoplankton and found a range of 0.03% to 3.00%. In laboratory streams, photosynthetic efficiencies for periphyton communities under a range of light

intensities ranged from 2.0% to 4.0% (Beyers 1963). In natural streams, photosynthetic efficiencies have been observed to range from 0.1-2.7 in Blue River (Duffer and Dorris 1966), 0.5-3.6 in the Raritan River (Flemer 1970), 0.3-3.3 in the River Raba (Bombowna 1972), and 0.1-2.5 in Deep Creek (Dunn 1976). The higher efficiency observed in the old-growth forest section of Mack Creek was a reflection of the lower light levels in that site. Production was greater in the clearcut section, but photosynthesis was often light saturated. Therefore, there was an excess of light available in the clearcut and efficiencies of utilization of total light in the open site were lower.

The River Continuum Project (Vannote et al. 1980) used the forest site on Mack Creek as an example of an unperturbed, third-order stream in a coniferous forest. Their studies in 1976 and 1977 found similar seasonal trends in primary production to the patterns found in my study in 1975 (Sedell et al. 1975, Naiman and Sedell 1979, Naiman and Sedell 1980, Naiman and Sedell manuscript in preparation). They observed similar seasonal trends for standing crop of periphyton, primary production, community respiration, P/R ratios, and net daily metabolism. They also observed that primary production was correlated to light intensity. In general, though there were differences in absolute values, the findings of the River Continuum Project were comparable with the results I obtained for the forested section of Mack Creek.

The response of primary producers to clearcutting observed in Mack Creek was consistent with results of a simulation model of biotic processes in lotic ecosystems (McIntire and Colby 1978). The model simulated the response of a stream ecosystem to clearcutting for 6 years

after harvest. Annual gross primary production in the old-growth forested section of Mack Creek was $52.1 \text{ g m}^{-2} \text{ year}^{-1}$ and in the clearcut section the annual gross primary production was $129.2 \text{ g m}^{-2} \text{ year}^{-1}$. The model predicted that annual gross primary production in a forested site would be $71.1 \text{ g m}^{-2} \text{ year}^{-1}$ and in a 6 year old clearcut, $187.1 \text{ g m}^{-2} \text{ year}^{-1}$. Observed rates of production in the forest and the clearcut were 69% and 74% of the predicted behavior, respectively. Average standing crop of periphyton was 1.4 g m^{-2} in the forested section of Mack Creek and 1.9 g m^{-2} in the clearcut section. The model predicted that standing crops of periphyton of 1.0 g m^{-2} in the forest and 1.2 g m^{-2} in the clearcut. Observed standing crops of periphyton in the forest and clearcut were 140% and 158% of the predicted standing crops, respectively. The response of primary producers observed in Mack Creek was similar to the response predicted by the model. In addition to accurately predicting the increase in primary production, the model further predicted that the rate of production for the entire stream ecosystem would increase after clearcutting and that the system would become autotrophic. The results of the model suggested that biomass of vertebrate predators would increase after clearcutting; after revegetation, predator biomasses would be lower than those found in the old-growth forest. The model predicted that biomasses associated with grazing and invertebrate predation would increase, and biomasses associated with collecting and shredding would decrease. These results of the model were consistent with responses to clearcutting that were observed in Mack Creek.

The data from my study and litterfall data from watersheds in the H. J. Andrews Experimental Forest allowed me to develop estimates of inputs of total organic matter for the clearcut and old-growth forest sections of Mack Creek (Table 5). Annual totals of gross primary production, net community production, and net daily metabolism are reported, but gross primary production is used in the calculation of total organic inputs. Use of gross primary production is consistent with use of total allochthonous inputs because respiration losses are not included in either source of organic matter. Subsequent utilization of gross primary production through respiration by autotrophs or heterotrophs is not subtracted from the inputs because the estimate of total input of organic matter is intended to represent all energy sources available to the stream ecosystem. Drift leaving the forested section of Mack Creek was greater than the amount of organic matter transported from the clearcut section; therefore, there was a possible input of organic matter to the clearcut from drift. Because the old-growth forest section was continuous to the headwaters of Mack Creek, I assumed that transport into the study section in the forest was equal to transport out of the reach.

Total inputs of organic matter were lower in the clearcut section of Mack Creek than in the forested section; however, the relative contribution of allochthonous and autochthonous sources of organic matter shifted as a result of clearcutting. Annual primary production in the clearcut was 2.5 times greater than in the forest. Input of allochthonous organic matter in the open section was only 7% of that estimated for the old-growth forest section. Input of drift into the

Table 5. Inputs of organic matter into a clearcut and a forested section of Mack Creek. All inputs are expressed as g AFDW m⁻² year⁻¹.

Source	Old-growth	Clearcut
Gross primary production	52.1	129.2
NCPP	31.8	80.7
CR	43.2	111.4
NDM	8.6	17.8
*Litterfall	197.8	13.1
Drift	-	51.2
TOTAL	249.9	193.5
GPP/Detritus	0.26	2.01
GPP/Litterfall	0.26	9.86
GPP/Total Organic Matter	0.21	0.67

*Litterfall was estimated from 18 months of measurements from streams in three clearcuts that were less than 10 years old and three old-growth forests in or adjacent to the H. J. Andrews Experimental Forest (Dr. G. M. Ward, personal communication).

clearcut reach added an additional $51.2 \text{ g m}^{-2} \text{ year}^{-1}$ of detritus to the total input for the open site. Gross primary production accounted for 21% of the total input of organic matter in the forest and 67% of the total input into the clearcut. Total detrital inputs were four times the annual gross primary production in the forest section and one-half the annual gross primary production in the clearcut. Litterfall in the clearcut section was only one-tenth the annual gross primary production in the clearcut section; but litterfall was almost four times greater than annual gross primary production in the forest section. The major sources of organic matter in the two sites had shifted so that autochthonous organic matter made up more of the input in the clearcut as opposed to the old-growth forest section, in which allochthonous organic matter dominated the inputs.

The shift in sources of organic matter in the two sites affected higher trophic levels in Mack Creek. Other researchers in the International Biological Program studied aquatic insect, salamander, and cutthroat trout populations in Mack Creek. Total emergence of insects was estimated to be 3.7 times greater in the clearcut than in the forest section, $2.2 \text{ g m}^{-2} \text{ year}^{-1}$ and $0.6 \text{ g m}^{-2} \text{ year}^{-1}$, respectively (Dr. E. Grafius and Dr. N. H. Anderson, personal communication). Production of aquatic insects can be approximated by multiplying emergence by 4.5 (Speir and Anderson 1974); therefore, total production of aquatic insects in the clearcut was about $9.9 \text{ g m}^{-2} \text{ year}^{-1}$ and in the forest it was $2.7 \text{ g m}^{-2} \text{ year}^{-1}$. Standing crops of cutthroat trout in the clearcut section were two times the standing crops in the forest section, 12.2 g m^{-2} and 6.2 g m^{-2} , respectively (Aho 1976). Production

of trout in the clearcut section was 7.5 g m^{-2} as opposed to 2.6 g m^{-2} in the forest, a three-fold difference. Aho's study was followed by studies by Murphy (1979) that included standing crops of invertebrate predators, salamanders, and cutthroat trout. Biomass of predatory insects in the clearcut section of Mack Creek was 0.57 g m^{-2} in pools and 0.52 g m^{-2} in riffles; in the forest section, biomass of predatory insects was roughly half those in the clearcut, 0.34 g m^{-2} in pools and 0.17 g m^{-2} in riffles. Standing crops of salamanders, Dicamptodon ensatus, were 40% greater in the clearcut, with standing crops of 20.1 g m^{-2} in the clearcut and 14.4 g m^{-2} in the forest. Standing crops of trout were determined for 3 years after Aho's study and the same basic relationship continued. Biomasses of trout for each year for the clearcut and forest sections, respectively, were: 1974 - 10.1 g m^{-2} and 3.8 g m^{-2} ; 1975 - 6.9 g m^{-2} and 2.6 g m^{-2} ; and 1976 - 9.9 g m^{-2} and 4.4 g m^{-2} (Hall et al. 1978). From 1973 through 1976, trout biomass in the clearcut was always more than double the biomass of trout in the old-growth forest.

Production of the aquatic biota was generally greater in the clearcut section of Mack Creek than in the forested section. The enhanced production in the clearcut was not simply a result of more total organic matter; total inputs of organic matter were greater in the old-growth forest. However, the type of organic matter did change; allochthonous organic matter (leaves, needles, wood) comprised most of the input in the forest and periphyton made up most of the input in the clearcut. Insects that feed on periphyton would be expected to benefit from a change to autochthonous dominance. Many grazers and collectors

are multivoltine and, therefore, can have greater annual production for a given standing crop. Many of these same insects drift more readily than heavy-cased caddisflies and large insects that shred leaves and needles. Therefore, the drifting insects that depend on periphyton could more readily be fed on by trout, which feed mainly on drifting aquatic insects and terrestrial insects. In Mack Creek, the trout diet in the clearcut included a greater abundance of Chironomidae and Baetis, insects that generally fall into the category of grazers that are prone to drift (Aho 1976). Production of these insects would be enhanced by a shift to a system based more on primary production in the stream.

Insect communities in open streams have been found to have greater standing crops than insect communities in forested streams. Insect communities in streams in logged and unlogged watersheds were compared in 65 streams in California (Erman et al. 1977). In general, densities of aquatic insects were greatest in streams in clearcuts and lowest in streams that flowed through mature forests. In logged watersheds with bufferstrips, streams with narrow bufferstrips had insect densities that were more similar to open streams and streams with wide bufferstrips had insect numbers more like those found in forested streams. However, diversity of aquatic insect communities was lower in streams in logged watersheds. Streams in logged watersheds all had greater numbers of Chironomidae, Baetis, and Nemoura. These taxa are commonly grazers or collectors and, in general, feed on periphyton. These are also taxa that Aho (1976) found in higher abundance in trout diets in the clearcut section of Mack Creek. Erman et al. (1977) found that higher

populations of aquatic invertebrates were related to higher biomasses; however, biomasses would not indicate the full magnitude of the responses to logging because many of the taxa that increased were small in size. Many of these smaller taxa were multivoltine, and increases in production of aquatic insects would not be reflected well in biomass of insects. The increased production of aquatic insects in response to clearcutting is not a result of a general increase in production of all taxa, but rather, an increased production of taxa that are supported by autochthonous primary production.

Production of predators in open streams may also increase as a result of greater autotrophic production. As previously described, invertebrate and vertebrate predators in Mack Creek had greater standing crops in the clearcut section than in the old-growth forest section (Aho 1976, Hall et al. 1978, Murphy 1979). This relationship of increased predator biomass in clearcuts was supported by a study of eight other pairs of clearcut and old-growth sections of first- to third-order streams in the McKenzie River drainage (Murphy 1979). Biomass of predators was greater in the clearcut section in eight of the nine streams. In the Polenz River in Germany, growth rates of brook trout were greater in two open, meadow sections than in a heavily shaded, forest section (Albrecht and Tesch 1961). In addition to greater growth rates of trout, higher standing crops of diatoms and aquatic insects were observed. In another European stream, Bere Stream in England, fish production was measured in three adjacent sections: an open, upstream site; a middle, forested site; and a lower, shrub-dominated site. Fish production was greatest in the

upstream site, followed by the shrub-dominated site, and least in the forested site (LeCren 1969). A similar relationship was observed in a stream in Scotland that also had an open, upstream site, a spruce-fir forest site, and an open meadow site (Mills 1969). Again, fish production was greatest in the two open sites and lowest in the forested site. In Spring Creek, Wisconsin, abundance and biomass of brook trout were monitored in a "Reference Zone" and a "Treatment Zone" for 3 years prior to streamside vegetation removal. All woody vegetation was cut in a 30-foot zone on both sides of the "Treatment Zone" and trout populations were monitored for 3 more years in both zones (Hunt 1978). In the "Treatment Zone," abundance of all age classes and total biomass of brook trout increased after removal of streamside vegetation. Prior to treatment, the "Treatment Zone" contained 26% more trout per acre than the "Reference Zone;" after treatment, the "Treatment Zone" held 83% more trout than the "Reference Zone." After removal of riparian vegetation, the "Treatment Zone" had 111% more trout over 6 inches in length than the "Reference Zone," although prior to treatment it had 4% less than the "Reference Zone." Instream vegetation increased by 15% after removal of streamside vegetation. Open streams with greater autochthonous primary production appear to have a greater potential capacity for production of higher trophic levels. In cases where predators in streams are food limited, shifts to greater inputs of autochthonous production may enhance production of predators.

The quality and dynamics of allochthonous and autochthonous sources of organic matter differ greatly and may influence the structure

and processing in stream ecosystems. Clearcutting in Mack Creek resulted in increased standing crops and production rates of primary producers as compared to the old-growth forest condition. The enhanced autotrophic production in the open site was reflected in greater production of aquatic insects, salamanders, and cutthroat trout. The responses observed in Mack Creek were not simply responses to clearcutting; similar responses have been observed in open and shaded streams throughout North American and Europe. Forested streams may be typical of the unperturbed state in many parts of the world, but forested streams are not necessarily more productive (Minshall 1978). Streams that are exposed to higher light intensities, whether as a result of man's activities or natural causes, have greater potential for autochthonous primary production, an energy source that may play a major role in determining the structure and function of stream ecosystems.

PRIMARY PRODUCERS IN STREAM ECOSYSTEMS

The major advancement in stream ecology in the last 20 years has been the realization that stream ecosystems are supported by two major sources of organic matter, allochthonous material from the adjacent terrestrial landscape and autochthonous material produced by aquatic plants in the stream (Hynes 1963, Cummins 1974, Vannote et al. 1980). Unfortunately, the recently-recognized importance of allochthonous organic matter in streams has overshadowed the more significant concept of the duality of energy sources. Small woodland streams have been adopted as the basic paradigm of the stream ecosystem, a view that is unnecessarily restrictive and nearly negates the interpretive value of a concept of dual sources of energy. The basic concepts of heterotrophy and autotrophy have been used interchangeably with allochthonous and autochthonous, which leads to confusion and hinders our understanding of processes and dynamics of stream ecosystems (Minshall 1979). Better understanding of allochthonous and autochthonous organic matter and the dynamics involved in their production and utilization in stream ecosystems will greatly strengthen the conceptual framework on which the science of stream ecology is built.

The terms allochthonous and autochthonous indicate the source of material in stream systems. Allochthonous is defined by Webster's Dictionary as "formed elsewhere than in situ" and autochthonous is defined as "formed in the place where it now occurs." In stream ecosystems, allochthonous material is that which has been formed in the terrestrial system and then enters the aquatic system; autochthonous material is that which is formed in the stream system and is generally

used to refer to primary production. Detritus can be either allochthonous or autochthonous, depending on where it was originally formed; detritus is not synonymous with allochthonous organic matter. The characteristics of allochthonous and autochthonous organic matter differ; therefore, the origin of organic matter plays a major role in determining the structure and dynamics of stream ecosystems. Imprecise use of the terms allochthonous and autochthonous can only lead to ambiguity in conceptual development in stream ecology and must be avoided.

Autotrophy and heterotrophy are terms that describe the general balance between primary production and total respiration within the stream system. As defined in Webster's dictionary, autotrophy is the condition of "needing only carbon dioxide or carbonates as a source of carbon and a simple inorganic nitrogen compound for metabolic synthesis;" heterotrophy is defined as the condition of "requiring complex organic compounds of nitrogen and carbon for metabolic synthesis." Plants are generally considered to be autotrophs and animals are heterotrophs. These terms have been applied to ecological systems to describe the degree to which primary production in the system can balance the total respiratory demand in the system. A system in which gross primary production exceeds total community respiration has a P/R ratio of > 1.0 and is considered autotrophic. A system in which gross primary production is less than total community respiration has a P/R of < 1.0 and is considered heterotrophic. Autotrophy or heterotrophy do not describe the sources of energy bases in streams. A stream can be heterotrophic and still derive almost all of its energy from aquatic primary production. Heterotrophic simply means that gross primary

production alone cannot supply all of the respiratory demands of the community. Often P/R ratios are determined for a short interval of time and do not reflect the long term P/R ratio. Storage of either allochthonous or autochthonous detritus will affect observed P/R ratios, yet P/R ratios alone can reveal nothing about storage or the type of material in storage. It is often stated that most stream ecosystems are heterotrophic and this is commonly true. However, this is often taken to mean that allochthonous organic matter plays a predominant role in supporting the stream ecosystem, a conclusion that is by no means supported by the original statement. That particular erroneous implication is often used as a justification for studying allochthonous detritus in streams. As a result of this misinterpretation, many stream ecologists have not vigorously attempted to examine the relative contributions of allochthonous and autochthonous organic matter in a wide range of stream sizes and types and to understand the implications of relative dominance of either of these energy sources on the structure and function of stream ecosystems.

The first attempts to quantify the absolute and relative contributions of organic matter from different sources to stream systems were directed to springs, the simplest, most manageable units available (Teal 1957, Odum 1957, Tilly 1967). The springs that Teal (1957) and Tilly (1967) studied were almost point sources and material balances were greatly simplified. These springs were in woodlands and the material balances demonstrated that allochthonous organic matter was the dominant source of energy. Odum (1957) developed a material balance for Silver Springs, Florida, a large open spring system that was dominated by aquatic primary production.

In efforts to develop organic budgets for stream systems, ecologists next turned to first-order, woodland streams (Fisher and Likens 1973, Sedell et al. 1974). The small size and flow of such streams permitted small groups of investigators to obtain complete budgets of organic matter inputs, storage, and outputs. These streams were heavily shaded and received large inputs of allochthonous organic matter, simply as a function of their small size and wooded location. Allochthonous organic matter accounted for more than 98% of the total input of organic matter in these streams, Bear Brook, New Hampshire, and Watershed 10, Oregon.

In larger streams, the canopy over the stream separates and higher light intensities reach the streambed; as a result, autochthonous primary production is greater than in shaded conditions and can contribute relatively more to the energy base of the stream. In Mack Creek, aquatic primary producers provided 21% of the total inputs of organic matter in the old-growth forest; however, in the clearcut, autochthonous primary production accounted for 67% of the total input of organic matter. In New Hope Creek, a low-gradient, third- to fourth-order stream in North Carolina, autochthonous primary production supplied approximately one-third to one-half of the energy base of the stream (Hall 1972).

In the Fort River, Massachusetts, a fourth-order river, input of allochthonous litter was $384 \text{ g m}^{-2} \text{ year}^{-1}$ and gross primary production was $610 \text{ g m}^{-2} \text{ year}^{-1}$; however, the annual P/R ratio was 0.5, indicating that allochthonous organic matter was needed to support at least half of the total stream metabolism (Fisher 1977). Minshall (1978) found that autotrophic production accounted for more than 99% of the total organic inputs in three reaches of Deep Creek, Idaho. In Tecopa Bore,

California, a desert spring-fed stream, aquatic primary production was the only source of organic matter (Naiman 1976). In the Red Cedar River, Michigan, gross primary production and total energy required by the heterotrophic community was determined; the amount of allochthonous material needed to meet the total stream metabolic demand was calculated by difference (King and Ball 1967). Excluding a reach that received sewage effluents, autochthonous primary production in four separate reaches was sufficient to support an average of 84% of the total metabolic demand of the stream ecosystem. Approximately 40% of the organic input to Bere Stream, England, was estimated to be autochthonous in origin (Westlake et al. 1972). Leaf fall was a small portion of the allochthonous organic matter; cress-beds accounted for almost half of the allochthonous input. In the Middle Oconee River, Georgia, a river approximately 50 m in width, autochthonous primary production supplied 33% of the total energy required by higher trophic levels (Nelson and Scott 1962). Standing crop of aquatic primary producers in a small stream in Kentucky, Morgan's Creek, was approximately 12 to 19 kcal m⁻² and standing crop of allochthonous leaf material was 4.7 to 13 kcal m⁻² (Minshall 1967). However, analyses of gut contents indicated that the majority of the food base for primary consumers was allochthonous leaf material. In the River Thames, a ninth- to twelfth-order river in England, 85% of the energy base of the river was of autochthonous origin, largely planktonic algae. Therefore, as streams and rivers widen or as man alters streamside vegetation, the potential contribution of aquatic primary producers to energy bases of streams increases.

Energy bases of small, headwater streams are dominated by allochthonous organic inputs; intermediate sized streams have significant contributions of both allochthonous and autochthonous organic matter (between 25% and 75% for either source); in large rivers, autochthonous primary production is the dominant source of organic matter, but mainly in a detrital form. This general trend in nature of organic matter inputs in streams from the headwaters to the ocean was a major component of the conceptual framework of the River Continuum Project (Vannote et al. 1980). Such a hypothetical scenario provides a template upon which to view the nature of biotic communities in stream systems: an abundance of detritivores feeding on large and fine particulate organic matter from allochthonous sources in headwaters, a mixture of detritivores and grazers in the intermediate sized streams with fine particle collectors feeding on both allochthonous and autochthonous material, and in the large rivers, a dominance of fine particle feeders. Many factors affect the absolute amounts of organic matter inputs along this trajectory and it is beyond the scope of this hypothetical trend to predict the total input of organic matter to stream reaches. However, this hypothetical continuum of allochthonous and autochthonous inputs of organic matter describes the changing nature of organic material from small streams to large, a change that can greatly affect the biotic structure of stream ecosystems.

The quality as well as the quantity of organic matter inputs influence the processes and dynamics of stream ecosystems. In Mack Creek, the total input of organic matter was actually less in the clearcut than in the old-growth forest, but the shift to greater inputs

of autochthonous organic matter in the open section resulted in greater production of aquatic insects, salamanders, and cutthroat trout.

Responses to change in sources of organic inputs are functions of the different physical, chemical, and biological characteristics of allochthonous and autochthonous organic matter. The two types of organic matter have both desirable and undesirable attributes as food sources in stream ecosystems (Table 6).

Nitrogen is a major determinant of food quality of organic matter for consumers (Kaushik and Hynes 1971, Triska et al. 1975). Consumers require C/N ratios less than 17 in their food; otherwise, they develop protein deficiencies (Russell-Hunter 1970). Allochthonous organic matter commonly has C/N ratios ranging from 200 to 25 (Triska et al. 1975), well above the necessary ratio of 17. Consumers of this material with high C/N ratios must differentially assimilate the associated microflora that develop on allochthonous detritus in streams through time. Primary producers in streams, on the other hand, have low C/N ratios, ranging from 6-15 (McMahon et al. 1974), well below the ratio of 17. Therefore, aquatic primary producers are richer sources of nitrogen than most allochthonous organic inputs.

Aquatic primary producers have different structural characteristics than allochthonous detritus. Allochthonous organic matter is mainly composed of leaves, needles, and wood, material that tends to be highly lignified. Algae, moss, and aquatic macrophytes, on the other hand, do not have lignified tissue. Lignin compounds are resistant to breakdown; therefore, allochthonous detritus is more difficult to utilize than autochthonous primary producers. Aquatic insects

Table 6. Comparison of attributes of major food bases in streams.

	Benthic Algae	Vascular Macrophytes	Allochthonous Detritus
C/N Ratio	Low	Low	High
Degree of Lignification	No Lignin	No Lignin	Lignified
Turnover Rate	Fast	Medium	Dead - No Turnover
Retention Mechanisms	Attached	Rooted	Not Attached - Passive
Particle Size	Microscopic	Macroscopic	Macroscopic
State at Consumption	Alive or Dead	Generally Dead	Dead
Need for Conditioning	Conditioning Not Required	Conditions Rapidly	Conditions Slowly
Suitability as Habitat for Aquatic Invertebrates	Provides Minimal Habitat	Provides Habitat	Provides Habitat
Standing Crop	Low	High	High
Resistance to Perturbation	Low	High	High
Rate of Recovery After Perturbation	Fast	Moderate	Slow

consumed greater amounts of filter paper that had been exposed to acidic fumes than untreated filter paper (Barlocher and Kendrick 1973). This response suggests that structural integrity of organic matter is also a factor affecting food quality. In this respect, non-lignified algal material would present less structural resistance to ingestion by aquatic invertebrates than allochthonous organic matter and would be better quality food.

Because of high C/N ratios and refractory compounds, a period of microbial colonization or conditioning time is necessary before allochthonous detritus is suitable for consumption (Cummins et al. 1973). No such lag time is necessary before consumption of benthic algae, but some degree of conditioning is necessary for mosses and aquatic macrophytes (Sudo et al. 1978). However, this lag time would be much shorter for aquatic macrophytes and mosses than for terrestrial material because aquatic plants are generally less lignified and, therefore, would become suitable food more rapidly.

Particle size of organic matter may also be a factor in the utilization of organic matter by consumers. Benthic algae are generally microscopic and in the approximate size range of the mouth openings of most aquatic invertebrates. Aquatic macrophytes, mosses, and most allochthonous detritus are macroscopic and require physical breakdown before they can be ingested. Though scraping, collecting, and shredding all have inherent metabolic costs, handling costs of processing large particulate organic matter are probably greater than for small particles.

Retention, storage, and recovery patterns of organic matter play important roles in determining suitability for food. Benthic algae

and living macrophytes and mosses are usually attached and are partially resistant to removal by currents. Allochthonous detritus and dead macrophytes are not attached and are more vulnerable to being swept away by fast currents. The attachment factor is overridden somewhat by the high standing crops of allochthonous detritus and aquatic macrophytes and mosses as compared to the relatively low standing crops of benthic algae. Intense surface scour may drastically reduce available algal material but detrital material that is removed by high flows will probably be replaced by redistribution of detrital material in storage in the sediments. After catastrophic removal of any organic material, either allochthonous or autochthonous, response time or recovery time is critical. Fast turnover times of benthic algae and moderate turnover times of aquatic macrophytes and mosses result in rapid recovery from perturbation, but the gradual input of allochthonous material results in much slower recovery for allochthonous components of stream ecosystems.

Because of the great number of differences between the characteristics of autochthonous and allochthonous organic matter and the profound impacts these differences can have on consumers in streams, the dominance of a particular source may strongly influence ecological attributes of stream systems. Margalef (1960) proposed a synthetic approach for describing the structure and dynamics of lotic systems and classifying lotic communities. His attempt was severely limited by his concept of the structure of stream communities; his basic division was benthic versus planktonic organisms. He dismissed the trophic approach from having any use in the regional classification of aquatic systems. Almost all of his classification was restricted to aquatic

primary producers and the downstream changes in taxonomic groups of algae, mosses, and macrophytes. The ratio of absorbance of pigment extracts at 430 nm and 665 nm was proposed as an index of the changes in these communities of primary producers. These changes were equated with changes in succession and maturity of stream communities. This system was examined in New Hope Creek, North Carolina (Motten and Hall 1972); differences in maturity as described by the ratio of 430/665 were overridden by local or edaphic factors. Margalef, himself, noted that environmental fluctuations may direct succession if frequent enough. The use of taxonomic distributions to describe the characteristics of stream ecosystems is too restricted to particular regions and has little explanatory value. Margalef (1963) later proposed several "unifying principles in ecology" that dealt with ecosystems in general and not just lotic systems. Mature ecosystems were described as more complex, composed of greater numbers of elements, having longer food chains, having organisms with longer life cycles, and having lower fecundity. The amount of primary production per unit biomass in mature systems was lower than in younger systems. These characteristics were included in a more extensive list of attributes of developmental and mature stages of ecosystems by Odum (1969). Many of the attributes that served to separate developmental and mature systems also serve to differentiate between stream systems dominated by autochthonous primary production and systems dominated by inputs of allochthonous organic matter (Table 7).

In general, stream systems dominated by aquatic primary producers have higher net production and lower standing crops of biomass. This

Table 7. Attributes of developmental and mature systems in a model of ecological succession that are also attributes of autochthonous and allochthonous-based systems (selected from Odum 1969).

Ecosystem Attributes	Developmental Stages	Mature Stages
Gross primary production/community respiration	Greater than 1.0	Approaches 1.0
Gross primary production/biomass	High	Low
Net community production	High	Low
Total organic matter	Small	Large
Inorganic nutrients	Extrabiotic	Intrabiotic
Species diversity	Low	High
Biochemical diversity	Low	High
Spatial heterogeneity	Poorly organized	Well organized
Niche specialization	Broad	Narrow
Size of organism	Small	Large
Life cycles	Short, simple	Long, complex
Mineral cycles	Open	Closed
Nutrient exchange rate	Rapid	Slow
Role of detritus in nutrient regeneration	Unimportant	Important
Growth form	For rapid growth (r-selection)	For feedback control (K-selection)
Stability	Poor	Good
Entropy	High	Low
	Autochthonous Systems	Allochthonous Systems

is consistent with changes observed in Mack Creek as a result of clearcutting. Autochthonous based systems have organisms with broad niches, small body size, and short simple life cycles. The response in Mack Creek of greater emergence of aquatic insects but only slightly greater standing crops in the clearcut is in agreement with this generalization. Stream systems with major inputs of autochthonous primary production have simple, linear food chains and less complex consumer communities as opposed to more weblike, complex food chains based on allochthonous organic matter. Communities of aquatic insects in streams in clearcuts generally have lower diversity of species but higher densities of individuals than communities in streams in old-growth forests (Erman et al. 1977). The same relationship has been observed in Mack Creek (Charles Hawkins, Oregon State University, personal communication). Therefore, many of the general attributes of developmental and mature systems serve to describe stream systems dominated by autochthonous or allochthonous organic matter. Changes observed in the standing crops and production of stream communities in Mack Creek as a result of canopy removal with general attributes that can be ascribed to systems based on either autochthonous or allochthonous organic material.

Concepts of ecosystem succession may have not been applied well to stream systems because researchers have tried to apply these concepts at too low a level of resolution. The dynamic, fluctuating nature of physical factors of stream communities may well override successional patterns within particular taxonomic groups. However, long term trends in trophic characteristics of stream systems may be adequately described

by concepts of ecosystems development. Streams cannot be considered in and of themselves but must be viewed at a higher level of resolution, as parts of the watersheds they drain. The nature of terrestrial ecosystems influences the intensities of light reaching streams, concentrations of nutrient entering streams, and the quality and quantity of allochthonous organic matter coming into streams. At times when terrestrial ecosystems are in pioneer stages, canopies over streams are reduced and more light reaches the streambeds; at the same time, nutrient outputs from watersheds are greatest. Potential for primary production is greatest under these conditions. Aquatic primary producers are simple forms of plants and have many of the attributes ascribed to pioneer communities. As forests develop, the canopies shade streams flowing through them and litter from terrestrial vegetation falls into the streams. The allochthonous inputs at these later stages simply reflect the nature of the terrestrial system. Therefore, it is only logical that autochthonous and allochthonous material should have many of the same attributes of developmental and mature systems that have been proposed for terrestrial ecosystems. Large rivers have less influence from terrestrial vegetation than low to intermediate order streams; therefore, large rivers would be less affected by succession of adjacent terrestrial ecosystems. However, in low to intermediate order streams, developmental patterns of stream communities may be best understood in terms of watershed processes and succession. Further, many of the attributes of the stream communities may be generalized from ecological concepts of ecosystem development.

Aquatic primary producers are a major component of stream ecosystems, sometimes playing a major role in supporting stream communities and sometimes playing a minor role. Even in a single stream, autochthonous organic matter may provide a substantial contribution to the energy base during one season but an insignificant amount in another season. A recent review of autotrophy in stream ecosystems found that P/R ratios in approximately half of all published studies exceeded 1.0, indicating that these streams were autotrophic at the time of measurement (Minshall 1978). Few of these estimates of P/R ratios were based on annual measurements; therefore, caution must be exercised in developing generalities from these findings. However, Minshall (1978) did find that autochthonous primary production accounted for a significant if not major portion of the total input of organic matter in all studies of relative inputs of allochthonous and autochthonous organic matter in streams, except for heavily shaded, first-order streams. Implications of increased aquatic primary production in streams include more than just response to quantity of inputs but also quality of inputs. Productivity of stream systems may be enhanced by shifts from allochthonous to autochthonous organic matter. Aquatic primary producers are an integral component of stream ecosystems and a major determinant of the nature and dynamics of higher trophic levels in streams. The dual nature of sources of organic matter in streams is a major characteristic of lotic systems and cannot be ignored if conceptual development in stream ecology is to be robust and progressive.

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Appendix A. Standing crops of chlorophyll a on artificial substrates in the study of light and nitrate effects on primary production in WS 10.

Site	Day	Chlorophyll <u>a</u> (mg m ⁻²)				
Ambient Light	7	0.0,	0.0,	0.0,	0.0,	0.0
Lighted	7	0.0,	0.0,	0.0,	0.0,	0.0
Lighted + NO ₃	7	0.0,	0.0,	0.0,	0.0,	0.0
Ambient Light + NO ₃	7	0.0,	0.0,	0.0,	0.0,	0.0
Ambient Light	14	0.0,	0.0,	0.0,	0.0,	0.1
Lighted	14	0.7,	1.2,	0.4,	0.5,	0.6
Lighted + NO ₃	14	1.7,	0.7,	2.2,	1.1,	1.3
Ambient Light + NO ₃	14	0.0,	0.0,	0.0,	0.0,	0.0
Ambient Light	21	0.0,	0.0,	0.0,	0.0,	0.1
Lighted	21	3.4,	1.8,	2.8,	5.0,	4.3
Lighted + NO ₃	21	13.3,	7.3,	10.7,	11.0,	9.9
Ambient Light + NO ₃	21	0.0,	0.0,	0.0,	0.3,	0.6
Ambient Light	28	0.3,	0.5,	0.4,	0.5,	0.5
		0.7,	0.3,	0.3,	0.3,	0.8
Lighted	28	3.4,	2.5,	2.5,	2.5,	2.1
		3.5,	2.4,	2.5,	3.4,	3.0
Lighted + NO ₃	28	9.0,	9.2,	13.4,	9.8,	14.0
		12.3,	12.3,	9.5,	10.2,	11.0

Appendix B. Metabolic response in the study of light and nitrate effects on primary production in WS 10.

Site	Gross Primary Production (mg C m ⁻² day ⁻¹)	Community Respiration (mg C m ⁻² day ⁻¹)	P/R
<u>WS 10, Forested</u>			
Ambient Light	2.4	3.8	0.63
	3.4	8.7	0.39
Lighted	28.0	33.4	0.84
	31.1	31.0	1.07
Lighted + NO ₃	82.3	47.3	1.74
	96.7	57.1	1.70
Ambient Light + NO ₃	2.1	4.4	0.48
	3.5	5.2	0.67
<u>WS 10, Clearcut</u>			
Shaded	6.2	18.0	0.34
	10.9	20.3	0.54
Open + NO ₃	19.1	23.2	0.82
	25.4	30.0	0.85
Open + NO ₃	31.4	20.0	1.57
	46.6	27.9	1.67
Shaded + NO ₃	5.9	13.9	0.42
	9.1	19.3	0.47

Appendix C. Standing crop of chlorophyll, biomass, and B/C ratios in study of effects of grazing on primary production.

Channel	Day	Chlorophyll <u>a</u> (mg m ⁻²)	B/C Ratio	Biomass (g m ⁻²)
SD ₀	0	34.0, 22.7, 22.2	71	2.42, 1.61, 1.57
SD ₁	0	29.6, 33.9, 28.4	81	2.39, 2.74, 2.30
SD ₂	0	29.6, 18.4, 18.6	81	2.39, 1.49, 1.50
SD ₇	0	28.4, 24.1, 19.4	79	2.24, 1.90, 1.53
SD ₁₃	0	32.5, 27.3, 24.1	74	2.40, 2.02, 1.78
SD ₀	10	75.4, 68.9, 72.4	100	7.54, 6.89, 7.24
SD ₁	10	73.4, 64.3, 77.7	95	6.97, 6.11, 7.39
SD ₂	10	61.2, 63.9, 62.0	89	5.44, 5.69, 5.52
SD ₇	10	53.1, 51.2, 46.9	79	4.19, 4.41, 3.71
SD ₁₃	10	15.1, 16.8, 18.2	74	1.12, 1.25, 1.35
SD ₀	15	105.8, 81.4, 64.6	138	8.92, 11.24, 14.61
SD ₁	15	82.0, 107.4, 74.6	123	10.08, 13.21, 9.17
SD ₂	15	66.2, 64.1, 60.1	108	7.14, 6.92, 6.50
SD ₇	15	73.5, 53.1, 38.7	79	5.81, 4.19, 3.05
SD ₁₃	15	7.2, 9.5, 15.1	74	0.53, 0.70, 1.12
SD ₀	20	110.3, - , -	148	20.08, - , -
SD ₁	20	83.0, - , -	118	11.53, - , -
SD ₂	20	74.3, - , -	134	9.66, - , -
SD ₇	20	61.3, - , -	79	4.85, - , -
SD ₁₃	20	8.4, 6.7, 11.5	74	0.62, 0.50, 0.85
SD ₀	25	117.3, - , -	182	21.34, - , -
SD ₁	25	90.9, - , -	139	12.64, - , -
SD ₂	25	109.8, - , -	130	14.28, - , -
SD ₇	25	40.0, - , -	79	3.16, - , -
SD ₁₃	25	10.4, 10.7, 10.7	74	0.77, 0.79, 0.79
SD ₀	35	114.1, 113.2, 172.9 204.1	136	15.52, 15.40, 23.51 27.70
SD ₁	35	189.4, 201.9, 189.4 126.6	144	27.27, 29.07, 27.27 18.23
SD ₂	35	176.6, 126.6, 155.0 159.5	123	21.73, 15.58, 19.07 19.65
SD ₇	35	65.3, 42.9, 38.3 31.1	81	5.29, 3.48, 3.10 2.52
SD ₁₃	35	6.2, 5.5, 8.4 4.5	67	0.41, 0.37, 0.56 0.30

Appendix D. Metabolic rates in the study of effects of grazing on primary production. Chlorophyll a and biomass estimates apply to the particular tiles that were being used for metabolic measurements.

Channel	Day	Chlorophyll <u>a</u> (mg m ⁻²)	Biomass (g m ⁻²)	P/R	Gross Primary Production (mg C m ⁻² day ⁻¹)	Net Community Primary Production (mg C m ⁻² day ⁻¹)	Community Respiration (mg C m ⁻² day ⁻¹)
SD ₀	0	28.1	2.00	2.74	223.6	182.8	81.6
SD ₁	0	29.5	2.39	2.68	199.0	161.8	74.3
SD ₂	0	30.6	2.48	2.95	242.2	201.2	82.0
SD ₇	0	22.0	1.74	3.19	194.8	164.2	61.1
SD ₁₃	0	26.9	1.99	2.54	214.1	171.9	84.4
SD ₀	15	64.7	8.93	2.11	443.3	338.4	209.9
		93.8	12.94	2.46	427.7	340.6	174.2
SD ₁	15	88.1	10.83	3.27	525.8	445.4	160.8
		91.1	11.21	3.64	551.5	475.8	151.3
SD ₂	15	65.3	7.05	4.65	478.4	427.0	102.8
		60.3	6.51	4.50	421.9	375.1	93.7
SD ₇	15	55.2	4.36	4.48	286.1	254.1	63.9
		74.8	5.91	5.09	380.6	343.2	74.8
SD ₁₃	15	12.3	0.91	2.52	196.1	157.2	77.8
		11.8	0.87	3.13	190.3	159.9	60.7
SD ₀	35	159.4	21.68	3.68	637.4	550.8	173.1
		143.3	19.49	3.70	582.3	503.6	157.4
SD ₁	35	158.5	22.82	4.23	535.4	472.2	126.5
		196.0	28.22	3.74	768.2	665.5	205.4
SD ₂	35	143.3	17.63	3.11	822.1	689.9	264.4
		88.5	10.88	3.63	438.1	377.7	120.7
SD ₇	35	37.1	3.00	4.48	338.7	296.2	86.0
		52.1	4.22	2.25	346.0	247.3	197.3
SD ₁₃	35	7.6	0.51	4.50	176.6	156.9	39.2
		4.2	0.28	2.17	102.3	78.7	47.2

Appendix E. (continued)

Source of Variation	df	SS	MS	F
<u>Net Daily Metabolism</u> SD_0, SD_1, SD_2				
Between snail densities	2	16346.3	8173.2	2.11 n.s.
Between dates	1	50700.0	50700.0	13.10**
Interaction	2	7737.7	3868.9	0.53 n.s.
Error	6	43433.7	7238.9	
<u>Total</u>	<u>11</u>	<u>118217.7</u>		
<u>Turnover Time</u> $SD_0, SD_1, SD_2, SD_7, SD_{13}$				
Between snail densities	4	561.7	140.4	6.68**
Between dates	1	43.3	43.3	2.06 n.s.
Interaction	4	84.1	21.0	9.10***
Error	10	23.3	2.3	
<u>Total</u>	<u>19</u>	<u>712.4</u>		
<u>Turnover Time</u> SD_0, SD_1, SD_2				
Between snail densities	2	91.6	45.8	3.7 n.s.
Between dates	1	99.0	99.0	8.0*
Interaction	2	24.8	12.4	4.0 n.s.
Error	6	18.4	3.1	
<u>Total</u>	<u>11</u>	<u>215.4</u>		

*** p < 0.005
 ** p < 0.01
 * p < 0.05
 n.s. not significant

Appendix E (continued)

Source of Variation	df	SS	MS	F
<u>Net Community Primary Production</u> SD_0, SD_1, SD_2				
Between snail densities	2	13351.8	6675.9	4.03 n.s.
Between dates	1	61246.9	61246.9	37.00***
Interaction	2	3314.2	1657.1	0.14 n.s.
Error	6	70361.4	11726.9	
Total	11	148274.3		
<u>Community Respiration</u> $SD_0, SD_1, SD_2, SD_7, SD_{13}$				
Between snail densities	4	38471.5	9617.9	3.08 n.s.
Between dates	1	3033.1	3033.1	0.97 n.s.
Interaction	4	12509.5	3127.4	1.50 n.s.
Error	10	20827.7	2082.8	
Total	19	74841.8		
<u>Net Daily Metabolism</u> $SD_0, SD_1, SD_2, SD_7, SD_{13}$				
Between snail densities	4	277978.8	69494.7	6.15**
Between dates	1	17946.0	17946.0	1.59 n.s.
Interaction	4	45200.0	11300.0	2.02 n.s.
Error	10	55890.1	5589.0	
Total	19	397014.9		

(continued)

Appendix E. Two-way analysis of variance of metabolic rates at different snail densities in the study of the effects of grazing on primary production.

Source of Variation	df	SS	MS	F
<u>Gross Primary Production</u> $SD_0, SD_1, SD_2, SD_7, SD_{13}$				
Between snail densities	4	494508.6	123627.2	11.31 ^{***}
Between dates	1	34802.8	34802.8	3.18 n.s.
Interaction	4	43732.5	10933.1	0.98 n.s.
Error	10	111635.9	11163.6	
Total	19	684679.8		
<u>Gross Primary Production</u> SD_0, SD_1, SD_2				
Between snail densities	2	11690.6	5845.3	4.63 n.s.
Between dates	1	73042.0	73042.0	57.90 ^{***}
Interaction	2	2522.9	1261.5	0.07 n.s.
Error	6	104386.3	17397.7	
Total	11	191641.8		
<u>Net Community Primary Production</u> $SD_0, SD_1, SD_2, SD_7, SD_{13}$				
Between snail densities	4	381061.2	95265.3	9.25 ^{***}
Between dates	1	26078.7	26078.7	2.53 n.s.
Interaction	4	41205.0	10301.3	1.31 n.s.
Error	10	78595.8	7859.6	
Total	19	526940.7		

(continued)

Appendix F. Standing crops of chlorophyll a, rates of primary production and respiration, and P/R ratios in the clearcut and old-growth forest sections of Mack Creek from November 1974 through October 1975. The single estimates of chlorophyll following the rates of metabolism refer to standing crops on substrates used in measurements of metabolism.

Date	Site	Chlorophyll <u>a</u> (mg m ⁻²)	Gross Primary Production (mg C m ⁻² day ⁻¹)	Net Community Primary Production (mg C m ⁻² day ⁻¹)	Community Respiration (mg C m ⁻² day ⁻¹)	Chlorophyll <u>a</u> (mg m ⁻²)
Nov.	MF	37.9, 32.4, 41.8	48.25	13.97	91.40	37.89
	MCC	41.3, 46.2, 39.9	124.08	54.52	185.71	41.32
Dec.	MF	16.3, 17.8, 13.4	6.75	-1.01	20.69	14.28
	MCC	14.3, 12.1, 15.8	-	-	-	-
Jan.		-	-	-	-	-
		-	-	-	-	-
Feb.	MF	9.1, 7.7, 10.1	6.74	5.25	4.48	9.10
	MCC	11.6, 13.4, 10.2	56.85	31.64	67.22	11.58
Mar.		-	-	-	-	-
		-	-	-	-	-
Apr.	MF	12.3, 9.4, 14.7	43.18	35.63	16.47	12.29
	MCC	23.4, 27.7, 18.8	50.15	36.66	29.43	23.42
May	MF	7.7, 11.0, 13.8	73.19	46.69	45.42	15.16
	MCC	22.9, 24.6, 21.2	105.03	73.80	53.54	22.97
June	MF	44.4, 40.9, 50.5	44.28	23.04	34.00	44.43
	MCC	33.9, 41.2, 33.5	136.10	88.21	76.61	33.95
July	MF	36.7, 42.4, 35.7	-	-	-	-
	MCC	35.1, 38.8, 29.9	-	-	-	-
Aug.	MF	35.7, 40.2, 34.8	53.82	38.83	23.99	35.68
	MCC	32.1, 37.0, 30.3	132.93	73.76	94.67	32.11
Sept.	MF	39.2, 35.5, 31.3	59.58	35.12	48.91	39.20
	MCC	43.2, 45.4, 40.4	129.97	79.33	101.28	43.17
Oct.	MF	36.1, 38.1, 31.9	18.80	13.68	13.76	36.12
	MCC	44.1, 46.8, 39.5	37.30	27.93	20.99	44.10

Appendix G. Concentrations of nitrate, orthophosphate, alkalinity, and pH, light intensity, and temperature in the clearcut and old-growth forest sections of Mack Creek from November 1974 through October 1975.

Date	Site	Nitrate ($\mu\text{g } \ell^{-1}$)	Orthophosphate ($\mu\text{g } \ell^{-1}$)	Alkalinity ($\text{meq } \ell^{-1}$)	pH	Light Intensity (Langleys day^{-1})	Temperature ($^{\circ}\text{C}$)
Nov.	MF	29.3	51.4	0.234	7.177	15	4.9
	MCC	30.2	35.1	0.229	7.202	150	4.9
Dec.	MF	33.7	56.6	0.201	7.128	5	2.3
	MCC	-	-	-	-	-	-
Jan.	MF	-	-	-	-	-	-
	MCC	-	-	-	-	-	-
Feb.	MF	32.3	68.1	0.180	7.149	15	2.7
	MCC	28.2	79.6	0.210	7.137	75	2.7
Mar.	MF	-	-	-	-	-	-
	MCC	-	-	-	-	-	-
Apr.	MF	38.7	53.8	0.262	7.230	44	2.4
	MCC	35.3	61.7	0.246	7.221	363	2.4
May	MF	36.5	37.9	0.235	7.075	77	3.6
	MCC	37.4	38.5	0.227	7.298	627	3.6
June	MF	60.3	43.2	0.191	7.253	106	7.2
	MCC	9.9	39.2	0.201	7.321	657	7.4
July	MF	-	-	-	-	-	-
	MCC	-	-	-	-	-	-
Aug.	MF	26.0	44.0	0.343	7.540	44	11.3
	MCC	21.5	51.2	0.327	7.594	225	11.9
Sept.	MF	51.1	84.0	0.287	7.319	80	10.3
	MCC	38.4	64.7	0.269	7.480	477	10.6
Oct.	MF	66.0	16.6	0.250	7.281	40	5.1
	MCC	41.7	16.6	0.264	7.423	73	5.2