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ture. In all cases, net assimilation was measured, since losses of nitrogen were not determined.

Tissue analysis revealed that the plant material averaged 86.3% water and that ash and Kjeldahl nitrogen averaged 15.0 and 2.5% of the dry plant.

DISCUSSION

The data suggest that measurements of NO_3 and NH_4 uptake made during the afternoon are those that can be expanded to a daily rate most satisfactorily. The failure of *Ceratophyllum* to assimilate NO_3 in the dark may be due to lack of suitable sources of cellular energy or of an operational enzyme such as nitrate reductase.

Some of the differences in the rate of uptake observed here may be due to variability in the age of the material, its nitrogen content, or local nutrient depletion in the bottles, all of which could have an effect on the rate of assimilation. The diurnal uptake of ¹⁴C by *C. demersum* is also highly variable so that expansion of rates obtained during one period of measurement to the rate for an entire day is not realistic (Wetzel 1965).

Continuous NH_4 assimilation by *Ceratophyllum* probably plays an important role in determining the concentration of NH_4 in the water. Even if the quantity assimilated is much lower than that reported here, continuous uptake by this plant could strip NH_4 from the water as fast as it is released by the

processes of decomposition. This may also allow little time for nitrification. If this is true in environments receiving little exogenous NO_3 , then the assessment of nitrogen flow into this community may be considerably simplified.

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A DIRECT METHOD OF MEASURING BENTHIC PRIMARY PRODUCTION IN STREAMS¹

ABSTRACT

This paper describes a method of direct measurement of the primary production of the benthic algal community in the lotic environment that eliminates calculations of diffusion and is adaptable to the various chemical analyses used to indicate rates of production. Benthic algal communities have been shown to be highly productive and may be more so than phytoplankton in shallow embayments (Odum et al. 1959; Pomeroy 1959; Smalley 1959; Teal 1959). In the lotic environment the significance of the benthic primary community varies. In headwater streams, allochthonous material may be more significant as a primary food source than the benthic algae produced in the stream (Chapman and Demory

¹This technique was developed at Oregon State University, Corvallis, and supported by Research Grant WP 423, Federal Water Quality Administration.

1963). In other streams, the benthos makes up the dominant part of the algal community (Odum 1959) and may play a significant energetic role.

Many techniques for measuring production of benthic algal communities have been developed, several derived from those developed for planktonic communities. Among these are various harvest methods (although the results may be more indicative of standing stock than of production), evolution of oxygen (Odum and Odum 1955), uptake of carbon dioxide and of other macro- and micronutrients. Methods using isotopes, ¹⁴C and ³²P- PO_4 , have been recently introduced (Riley 1956; Steemann Nielsen 1952). There are advantages and disadvantages to all these methods, and no single one has been adequate in all situations.

The technique described in this paper, using a photosynthesis-respiration (P-R) chamber, is a modification of the lightand dark-bottle technique (Gaarder and Gran 1927). A bell jar modification of this technique was used by Odum and Odum (1955) in measuring the productivity of coral reef communities. The P-R chamber technique was first developed to measure production by benthic communities of the laboratory streams described by McIntire et al. (1964). It was later modified for use in an in situ study of the benthic algal community metabolism of small mountain streams (Hansmann 1969; Lane 1965).

DESCRIPTION OF THE AQUATIC ENVIRONMENT

The streams studied are part of the Drift Creek drainage of the Alsea Basin on the central Oregon coast, about 11 km inland from the Pacific Ocean and 16 km south of Toledo, Lincoln County, Oregon. The study sections were composed of riffles and pools that were moderately shaded throughout the year by the Douglas fir overstory and more extensively during the summer months when the understory was in leaf. Depth of water over the riffle varied with the season, ranging from 2.5–7.5 cm during summer to winter depths of 15–30 cm. The substrate consisted of cobbles and gravel, ranging from a few millimeters to 15 cm or more in diameter, of soft porous rock derived from the Tyee sandstone of the Coast Range.

Tow samples taken in the streams with a No. 20-mesh plankton net indicated that the streams were devoid of rheoplankton and contained only tycoplankton—those organisms dislodged from the benthic algal community. Data from artificial substrates indicated that the streams supported mainly a benthic diatom community. After clearcut logging of one of the watersheds in 1966, the stream supported a mixed community of diatoms and filamentous algae with the filamentous algae being the dominant component of the flora (Hansmann 1969).

METHOD

Porcelainized steel trays $(45.7 \times 45.7 \times 2.5 \text{ cm})$ were positioned in riffle areas, and rock and gravel from the surrounding streambed put into them. The disturbed benthic community in the tray was allowed to reestablish itself for 1 month before productivity was measured.

The tray was isolated from the stream by covering it with transparent plastic (Fig. 1), producing a chamber containing a portion of the benthic community on the rock substrate which was then filled with streamwater from an elevated reservoir. The water was circulated through plastic tubing connected to the front and back of the chamber to simulate turbulent mixing; the exchange was at a rate of 200 Three small centrifugal pumps ml/min. operated from a portable generator and continuously replenished the water in the elevated reservoir and circulated the water within the system. Temperature of the water in the stream, chamber, and reservoir was monitored hourly.

Changes in the concentration of dissolved oxygen in the chamber were mea-



FIG. 1. Diagram of the photosynthesis-respiration chamber.

sured by the Winkler method (Amer. Public Health Ass. 1960) from sample bottles attached to the influent and effluent exchange tubes of the chamber. Samples of the influent and effluent water were taken every hour, and measurements were continued for 8–12 hr in each sampling period (arranged to include both daylight and dark hours). This schedule allowed computation of hourly rates of photosynthesis and respiration. The change in oxygen concentration in the total volume of water in the chamber was then calculated by the method of McIntire et al. (1964).

Gross primary production per hour was estimated by adding mean community oxygen consumption during the dark period to the net oxygen evolved during photosynthesis (photosynthesis minus respiration). The rate of respiration in the dark was assumed to be the same as that during photosynthesis. Recent evidence suggests that this assumption may not be true (Jackson and Volk 1970); this problem may have to be resolved by partitioning the P-R chamber into a light and dark section and analyzing the rates of oxygen consumption and production simultaneously.

In initial trials, the water in the chamber became warmer than that of the stream by as much as 5C. This increase in temperature, assumed to be caused by characteristics of the plastic dome, caused streamwater entering the chamber to become supersaturated with oxygen; the excess oxygen was given off as masses of minute bubbles on the undersurface of the top of the chamber.

To eliminate supersaturation of the water with oxygen, a sparging column was installed in the influent waterline. The degree of reduction in the concentration of oxygen was determined by the temperature expected in the chamber that day. To control the temperature of the water

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in the chamber, a monel alloy cooling coil, placed in an ice-packed chest, was connected to the water circulation tubing of the chamber (Fig. 1). Water leaving the chamber through the circulating system was drawn through the coil and cooled before reentering the chamber. The flow of water entering the coil from the circulating tube was regulated by screw clamps. The temperature in the chamber could be controlled to within ± 0.5 C of that of the stream. With the addition of these two modifications, the problems encountered in the field appeared to be solved and the system performed adequately during the remaining period.

DISCUSSION

Several productivity runs were made in the streams during spring, summer, and fall 1967. The gross primary productivity. (g $O_2 m^{-2} day^{-1}$) ranged from 0.5–2.5 g $O_2 m^{-2} day^{-1}$, somewhat lower than reported by McIntire and Phinney (1965).

The P-R chamber technique for measuring primary productivity of benthic algal communities has wide application in the lotic environment. The productivity of the large assemblage of organisms making up the benthic community can be analyzed, and individual populations can be isolated and their contribution determined. Physical and chemical properties of the environment can be related to production rates. Isotopes may also be used in the P-R chamber. The chamber measures the production rates in streams directly, eliminating the effects of such factors as oxygen diffusion.

The system is limited to measuring only gross algal production as we cannot yet separate animal and plant respiration. Such separation would be useful because net production would add valuable data to the energetic dynamics of the lotic environment. The system appears to be sensitive to slight changes in dissolved oxygen, and is thus especially applicable to streams having scant amounts of organic material. ——, AND E. P. ODUM. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. **25**: 291–320.

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Photosynthesis and Respiration in *Myriophyllum spicatum* L. As Related to Salinity¹

ABSTRACT

After about 20 hr at low light intensity in the laboratory, photosynthesis was depressed in Myriophyllum spicatum tips at a salinity of 32%, but respiration was not affected. Neither photosynthesis nor respiration was depressed at salinities of 16% and less. When the plants were maintained on 10-14-hr light-dark cycles at moderate light intensities, after 48 hr and up to 10 days, photosynthesis was depressed at salinities of 16% below that of plants in Albemarle Sound water, although respiration remained high. The depression of photosynthesis at high salinity and its effect on the P:R ratio are assumed to play a part in controlling natural distribution of M. spicatum in estuaries.

Field observations in the Chesapeake Bay area indicate that the distribution of *Myriophyllum spicatum* L. (Eurasian watermilfoil) and many other macrophytes can be affected by salinity (Anderson 1964; J. H. Steenis, personal communication). The species is stunted or killed when the salinity is over 13-14%. In addition to the effect of normal salinity gradients on the growth and distribution of *M. spicatum* in estuaries, drastic salinity changes associated with seawater intrusion can result in eradication of the plant.

The mechanisms by which supraoptimal salinities affect the distribution of higher plants occurring mainly in freshwater are not known, but as Sculthorpe (1967) pointed out, they are probably varied and complex. We report here experiments designed to show the effects of increasing salinities on photosynthesis and respiration and, therefore, on the P:R ratio in M. spicatum.

MATERIALS AND METHODS

Vegetative, floating fragments of M. spicatum about 15-20 cm long were collected in June along the southern shore of Albemarle Sound, North Carolina, near the mouth of the Alligator River where the weed has recently become established. These were maintained for 3 weeks in sound water in an aquarium growth chamber. The salinity of the water was 1%. Illumination was provided by diffuse fluorescent light supplemented with incandescent light giving around 2 mW/cm² at the water surface as measured with a radiometer. Light periods of 8 hr alternated with 16-hr dark periods. The daily variation in temperature of the water was 16-21C with the warmer temperatures during light periods.

About 20 hr before each run, tips 2 cm long were removed and placed singly in test tubes in a series of artificial seawater (Seven Seas) solutions (group I) or in a series of Albemarle Sound water—artificial salt solutions (group II). The sound water was filtered and kept refrigerated until used. Salinities in each group were at 0, 4, 8, 16, and 32‰. The 32‰ solution of group II was prepared by adding salts

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