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Measurement of photosynthetic carbon fixation in aquatic systems

1. Principle of measurement

The photosynthetic carbon fixation of autotrophic plants and bacteria is called primary production, since this process produces first organic compounds formed out of H_2O and carbon dioxide. The actual primary production rate depends on many factors such as temperature, incident light, availability of nutrients and the biomass and metabolic status of the primary producers. In the aquatic environment, it can be measured as the uptake of inorganic radiocarbon (^{14}C) by aquatic autotrophic organisms. The radiocarbon method was introduced into limnology by Steemann Nielsen (1952). Several reviews on possibilities and restrictions of the method are given in the literature (e.g. Coljin 1983, Harris 1984, Maestrini et al. 1993, Peterson 1980). Up to today, it is one of the most sensitive methods for the determination of primary production.

For the measurement of primary production, trace amounts of $NaH^{14}CO_3$ are added to the sample. The incorporation into biomass is determined either by filtration of particulate matter and measurement of its radioactivity or by the acidification and bubbling technique which measures both particulate and dissolved production. Under the assumption that ^{14}C is fixed with a comparable rate as ^{12}C, the carbon fixation rate can be calculated from the ^{14}C incorporation and the concentration of dissolved inorganic ^{12}C.

Use of the radiocarbon methods need an approved radionuclide laboratory. In Germany, use, storage, transport and disposal of radioactive isotopes are controlled by official federal regulations. Investigations using radiocarbon need permission if they exceed a rather low quantity.

Primary production measurements with the radiocarbon method are carried out in enclosed samples of pelagic as well as of benthic communities, incubation can occur in shipboard or laboratory incubators or *in-situ*. The radiocarbon method is suitable for primary production measurement in oligo- to hypertrophic water bodies. Coloured samples require an effective quench correction for the liquid scintillation counter. In acidic samples with low DIC-concentration (< 1 mg l^{-1}), a sensitive DIC-determination is necessary and the samples have to be handled carefully to avoid the loss of added $^{14}CO_2$.

2. Measured processes

Fixation of inorganic carbon takes place in the Calvin-Benson cycle and is catalysed by the enzyme ribulose biphosphate carboxylase. In eucaryotic algae, these reactions occur in the chloroplast stroma (Falkowski & Raven 1997). As well as photoautotrophic eucaryotes and procaryotes, chemolithoautrophic organisms are capable to fix inorganic carbon by anoxygenic photosynthesis.

Interpretation of primary production measurements can be made more difficult by the metabolic fate of the fixed ^{14}C. A part of the previously assimilated ^{14}C can be respired, depending on incubation time and metabolic activity of the investigated community. Another part of the fixed ^{14}C can be exuded as dissolved organic carbon or lost by breakage or lysis of cells. By removal of inorganic carbon from the sample by the acidification and bubbling method (Gächter et al. 1984, Riemann & Møller Jensen 1991, Schindler et al. 1972) exudation can be measured.

The amount of ^{14}C, which is respired or exuded, determines, whether net or gross primary production is measured by the radiocarbon method (Dring & Jewson 1982, Harris et al. 1989). Equilibrium between ^{12}C and ^{14}C inside the metabolic pools of phytoplankton can be reached after a period as short as two hours, but it may even take some days, depending on the metabolic activity of the phytoplankton.

Dark fixation of inorganic carbon usually occurs at a slow rate by organic and inorganic processes. The dark fixation rate is subtracted from the light fixation rates. As an alternative to dark incubated bottles, some authors prefer the use of DCMU (Yallop 1982, Legendre et al. 1983).

The slower uptake of ^{14}C compared to ^{12}C is usually corrected by the isotopic discrimination factor 1.06.

3. Different incubation methods

Three methods for estimation of integral primary production are in common use:

a) static incubation of several samples along a vertical profile in the euphotic zone *in-situ*,
b) dynamic incubation with vertical movement of samples through the euphotic zone *in-situ*, and
c) incubation in a light incubator with defined light intensities.

The traditional method of incubating several samples along a vertical depth profile to calculate the integral primary production has some disadvantages, which are independent of the used method (O_2 or ^{14}C). The measurement is laborious and time consuming (Nixdorf et al. 1990). The static exposition of samples in fixed depths does not meet the natural conditions in well mixed eutrophic water bodies. Algal movement induced by turbulence or active migration is suppressed. The algae are forced to stay under constant light conditions for several hours.

Dynamic incubation methods were developed to overcome these shortcomings. They are designed to imitate turbulent mixing to measure a more realistic primary production by consideration of vertical movement of algae in a mixed layer (e.g., Gervais et al. 1997). The measured value of production is an integral, describing the average of integral primary production within the zone, where the samples were moved.

There is a good agreement in many cases between the results of static and dynamic incubation. In some cases an enhancement or reduction of primary production by dynamic incubation could be observed. Dynamic incubation of just one sample suffices to measure areal production. In that way, radioactive material and filters as well as time can be saved.

The third incubation method is used to measure phytoplankton primary production under controlled light conditions in the laboratory (e.g., Tilzer et al. 1993). The so-called photosynthetron, a laboratory incubator, can be used to measure primary production by both ^{14}C-uptake and chlorophyll fluorescence. The relationship between light and photosynthesis can be used to calculate *in-situ* primary production. Important parameters for the calculation are the intensity and spectral

distribution of light, temperature and phytoplankton distribution in relation to depth. A model for calculation is given by Walsby (1997).

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