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Wetzel R G. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large, shallow lake. Internationale Revue der Gesamten Hydrobiologie 49:1-61, 1964. [Indiana University, Bloomington, IN]

This study described the first application of the <sup>14</sup>C uptake method to submersed angiosperms and attached algae in aquatic ecosystems. The seasonal and annual rates of primary productivity of the higher aquatic plants and sessile algae were compared to those of the phytoplankton and demonstrated the major contributions of the attached plants to the total lake productivity [The SCI® in-dicates that this paper has been cited in over 140 publications since 1964, making it one of the mostcited papers ever published in this journal.]

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"Most analyses (>99 percent) of the photosynthetic productivity of aquatic ecosystems focus on the phytoplankton of the open water. The productivity of the larger rooted aquatic plants and sessile algae on sediments and epiphytic on submersed portions of the macrophytes was largely ignored as insignificant to the whole, in spite of intuitive observations and more recent evidence to the contrary. At the time of my early analyses, I was convinced that the total emphasis on phytoplankton, spurred by the prevailing concerns of nutrient loading to lakes and their eutrophication, neglected a major source of organic production via the macrophytes and attached algae in most lakes. Evidence demonstrated that existing methods of analyzing in situ productivity of the attached forms, largely by changes in dissolved oxygen concentration, were erroneous for a number of physiological reasons. The <sup>14</sup>C uptake method for estimating in situ rates of photosynthesis was developed<sup>1,2</sup> in the 1950s for phytoplankton and has been widely used since that time, despite continuing interpretative problems. In order to adapt the <sup>14</sup>C method to attached plants, the

in situ incubations had to be modified greatly. In addition, the self-absorption of the weak radiation by the plant tissue required tedious chemical oxidation of the organic carbon and radioassay in gas phase in that period before the availability of tissue solubilizers<sup>3</sup> and liquid scintillation. Much knowledge has been gained since on the metabolism of submersed vascular plants, their photorespiration and efficient recycling of CO2 in internal lacunae, and the transport of CO<sub>2</sub> from respiratory sources in the rooting tissue and sediments,<sup>4</sup> some of which affects interpretation of the <sup>14</sup>C technique developed in this study.

"The lake selected for the analyses in northern California was typical in morphometry of many shallow lakes but was highly saline, which presented numerous chemical and analytical problems. Nonetheless, in spite of formidable problems of working alone from a small rubber life raft in extreme heat along a rattlesnake-infested shoreline, the comparative analyses did provide an often cited example of a since commonly demonstrated situation in which the primary productivity of the attached producers exceeded that of the phytoplankton. In addition, the paper contained a detailed critical review of various methods for analyses of attached macrophytes and algae, and the diverse littoral terminology that proved to be useful to others. The study provided evidence for the importance of littoral producers and perhaps incentive that these components cannot be neglected in most lake ecosystem analyses. The extreme heterogeneity found in the littoral biota and environmental factors in the water and sediments renders effective analyses of in situ littoral communities difficult. Sufficient evidence now exists to force us to recognize that these littoral and adjacent wetland communities can not only influence loading to the open water but often control much of the pelagic and benthic metabolism of lake ecosystems.5 This study provided one small step in the recognition of that importance."

<sup>1.</sup> Steemann Nielsen E. The use of radio-active carbon  $(C^{14})$  for measuring organic production in the sea. J. Conseil 18:117-40, 1952.

<sup>2. .....</sup> Citation Classic. Commentary on J. Conseil 18:117-40, 1952.

Current Contents/Agriculture. Biology & Environmental Sciences 11(17):12, 28 April 1980. 3. Beer S, Stewart A J & Wetzel R G, Measuring chlorophyll a and <sup>14</sup>C-labeled photosynthate in aquatic angiosperms by the use of a tissue solubilizer. Plant Physiol. 69:54-7, 1982.

<sup>4.</sup> Wetzel R G & Grace J B. Aquatic plant communities. (Lemon E R, ed.) CO2 and plants.

Boulder, CO: Westview Press, 1983. p. 223-8.

<sup>5.</sup> Wetzel R G. Limnology. Philadelphia, PA: Saunders, 1983. 860 p.