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*Consequences of Small Storage Capacity in
Nannoplankton Pertinent to Measurement of
Primary Production in Tropical Waters*¹

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ABSTRACT

A theory based on the performance of an electrical analogue circuit for balanced ecosystems relates respiration to the storage of labile organic matter during daytime photosynthesis. A very small storage capacitance and time constant may be introduced into the circuit to simulate a nannoplanktonic system. It is found that respiration approaches photosynthesis during the day and almost ceases at night. Consequently, the usual carbon¹⁴ measurements of net production, and the conventional light-and-dark-bottle oxygen measurements of net production and nighttime respiration greatly underestimate gross photosynthesis of tropical seas. An example of this phenomenon is shown in a planktonic brine microcosm.

INTRODUCTION

There is an increasing tendency in applied mathematics and engineering to substitute circuit diagrams for differential equations, not only in experimental work but in mathematical expression as well; this procedure is equally precise, much more condensed, and more capable of complex representation. Separate components of ecosystems concerned with the flow of carbon in biological cycles can be connected, and the separate physiological functions can be integrated by electrical circuits. In this paper, the circuit methodology is used to illustrate two basic functions—gross photosynthesis and community respiration—in order to obtain some hypothesis concerning net production during the daily cycle. This represents one effect, which, when placed with others, will integrate the many facets of the ecosystem. Olson (1959) provided a similar theory for seasonal changes in soil litter of forests although his analogue equivalents were different.

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DESCRIPTION AND EXPERIMENT

An Electrical Analogue Circuit and Theory. Fig. 1 shows a simple electrical analogue model for the primary-producer and consumer trophic levels connected as one circuit. Gross photosynthesis is represented by a battery (B) that is connected so that it simulates photosynthesis during daylight hours. First, gross production of labile organic matter (P), represented by electronic flow, goes to a storage capacitor (C) that represents mainly the plant cells

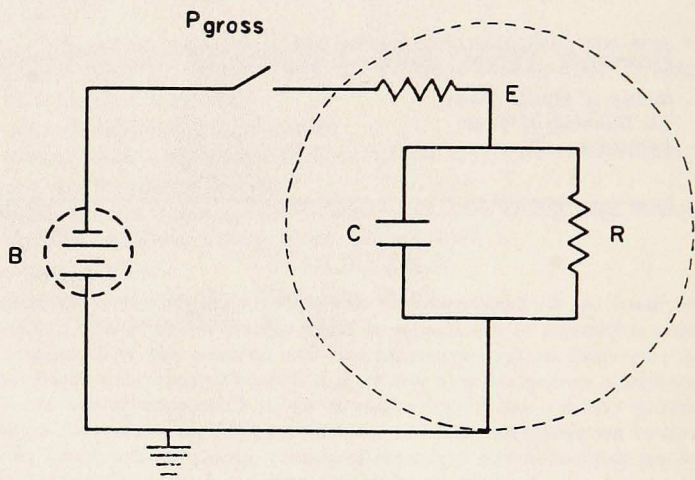


Figure 1. Electrical analogue circuit model for diurnal metabolism of balanced systems without net growth, export, reproduction, or loss to external consumers. The dashed circle on the left represents the components of the ecosystem with gross photosynthetic function; for the purpose of this study, gross photosynthesis is held constant or turned off. The dashed circle on the right represents the respiratory components of the ecosystem, including the respiratory tissues of the plants, the immediately related animals, and the microorganisms. The condenser represents the storage capacity of the respiratory system for recently produced labile organic matter.

and their capacity to take on the high energy compounds and organic matter just produced. Then, from this storage, with a rate proportional to the concentration of the labile organic matter stored, a circuit resistance (R) goes to the ground; this circuit represents daytime cellular respiration (mainly by the plant cells) which returns the organic carbon to the inorganic state of the ground reservoir. The difference between the rate of charging of the capacitor by the battery and the rate of loss of charge through the resistance is analogous to net production.

With the battery disconnected, the electrons stored in the condenser (E) bleed off through the resistance (R); this flow represents nighttime respiration. During either the simulated day or night, both the voltage on the con-

denser storage and the respiration (amperes at R) may be recorded by a recorder at E. Some additional discussion of this analogy in more complex circuits, and details of its pertinence to biological systems may be found elsewhere (Odum, 1960). Odum (1962) has subsequently elaborated on the analogy through the addition of reproduction to the system as a linear feedback to obtain a logistic growth curve.

Experimental Example. The output of the electrical circuit in Fig. 1 was recorded for different sized capacitors, and rates of change have been plotted in Fig. 2.

To illustrate the applicability of the analogue-circuit theory for a biological system with small capacitance, a brine microcosm was set up and adapted to a steady light regime so that the diurnal patterns of net production and respiration could be followed in a simple system not undergoing rapid growth. The water, sediment, and biota came from the Salina Fortuna Salt Works, near La Parguera, Puerto Rico. The microcosm contained water of 188‰ salinity at 23°C, subjected to 467 footcandles of fluorescent light on a 12-hour schedule alternating with 12 hours in the dark. This miniature ecosystem was housed in an all-glass aquarium 10×14.5×19 cm (depth). There were 3 cm of sediment and 10.5 cm of water. At the time of the measurement, the microcosm had been in existence three months and contained an approximate steady-state regime of *Dunaliella*, bacterial microorganisms, a few *Artemia*, and little else. Measurements of the diurnal carbon metabolism were made with the pH-CO₂ method (Beyers et al., 1963). The rate-of-change graph from a day-and-night metabolic sequence is plotted in Fig. 3. The separate points are computational results from the continuous pH record chosen at each curve inflection. The graph for the brine system, in Fig. 3, may be compared with the output of the analogue circuit with a small capacitance, in Fig. 2.

DISCUSSION

The Analogue of Diurnal Respiration. For the present discussion, consider systems in which there are little reproduction, accumulation, or loss to higher consumers outside the system. This situation is simulated in Fig. 1 and is exemplified by a closed nannoplanktonic microcosm having reduced higher trophic levels. One of the consequences of the analogue theory implied in the restricted model is a diurnal variation of system respiration that is dependent on the recent accumulations of labile products from gross photosynthesis. The storage of this organic material rises during the day as does the respiration that is dependent on that storage. Both storage and respiration are maximal at sunset and diminish logarithmically during the night. In a series of studies on 12 balanced aquarium microcosms, Beyers (1962a, b, 1963a) measured the variation in nighttime respiration in more than a hundred daily runs; he found

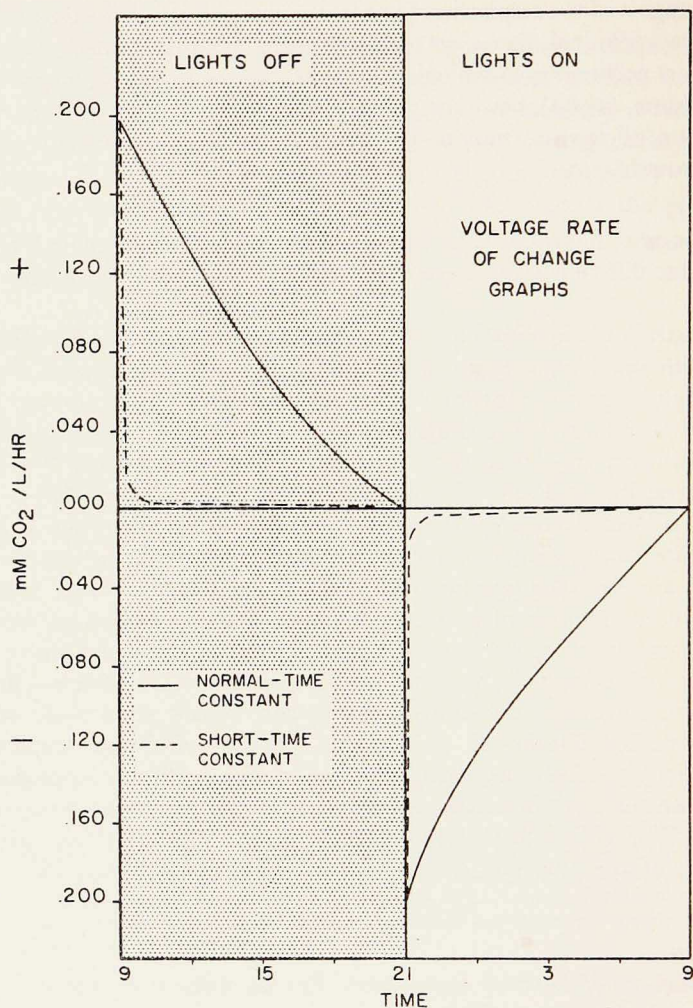


Figure 2. Diurnal rate-of-change graphs of voltage simulating the course of storage (net photosynthesis) and nighttime respiration in the circuit in Fig. 1. Results are expressed in units of simulated carbon metabolism. The diurnal graph with a very small storage capacity and high respiratory conductivity has the short-time constant graph simulating tropical nannoplanktonic systems.

that this pattern obtained 85.5% of the time. Supporting evidence from eight other types of ecosystems and symbiotic organisms was presented at the symposium on closed ecosystems at Corvallis, Oregon (Beyers, 1963b). These measurements provide some basis for application to the analogue model theory. The daily course of the rate of voltage change (storage and metabolism) with normal storage capacity is graphed in Fig. 2.

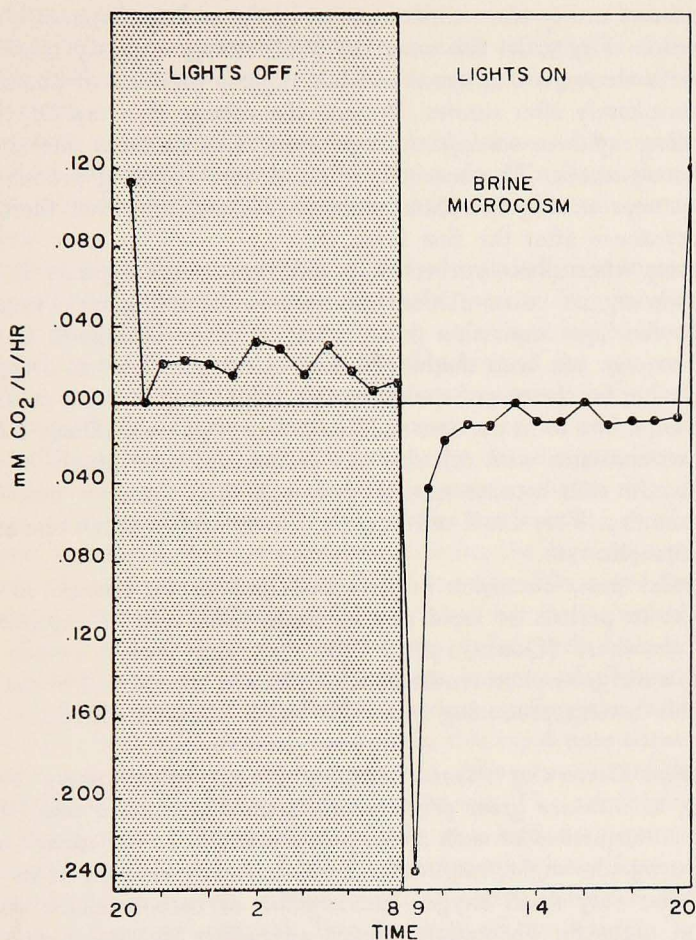


Figure 3. Diurnal rate of carbon uptake and release in net photosynthesis and nighttime respiration in a brine microcosm containing a planktonic system.

Small Capacitance and Time Constant with Tropical Nannoplankton. In oligotrophic tropical waters, phytoplankton numbers are small, and the mean cell size is smaller than in coastal, eutrophic, and temperate waters. In terms of the analogue model, the prevalence of sparse small cells such as these is equivalent to the substitution of very tiny condensers in the circuit; and the high prevailing temperatures that contribute to a high respiratory metabolism per unit organic matter are equivalent to a low resistance circuit (Fig. 1). The combination of small capacitance and low resistance is commonly described electrically as a circuit with a short-time constant.

The type of diurnal curve for photosynthesis and respiration that results

from the use of a very short time constant in the analogue system is extreme, as indicated in Fig. 2. In this case, the small storage capacity becomes fully charged with electrons that simulate labile organic products of photosynthesis almost immediately after sunrise. Because the voltage rises rapidly, there is a corresponding rapid rise in daytime respiration to a maximum rate that almost equals photosynthesis. The resultant of these two opposing processes is the dashed line representing net photosynthesis (Fig. 2); note that there is little net photosynthesis after the first hour.

At sunset, when photosynthesis cuts off, the storage capacity is so small that its labile organic accumulation (electrons in the analogue) is immediately bled off by the high respiration (low resistance in the analogue). In an hour the labile storage has been discharged, and the respiration has dropped to a negligible value for the rest of the night. The night respiration is consequently small in comparison to its daytime and immediate postsunset values. The variation in time constants with cell size can be inferred from graphs of size and metabolism. As cells become smaller than 5μ , their turnover time becomes less than one day. Very small cells may turn over hourly when operating at a normal metabolic rate.

The model under discussion here does not provide for changes in capacity diurnally as in periods of rapid reproduction. One type of reproduction is discussed elsewhere (Odum, 1962). Nor does this model include diurnal variations in the gross photosynthesis, which can be represented in the analogy as a variable battery producing somewhat more complex patterns.

Implications Concerning Measurements of Primary Productivity. For those attempting to measure gross primary production in tropical seas, there are important consequences of such a short-time constant in the capacitor circuit system. During the night, respiration drops to a tiny fraction of its daytime value, so that very small oxygen-consumption or carbon-release values are obtained at night for respiration. Hence any effort to correct daytime net photosynthesis with nighttime dark respiration vastly underestimates the actual gross production.

During the day the respiration rises immediately along with the gross production so that net storage of radio-carbon in the cells is small, and net photosynthesis almost ceases while a large gross photosynthesis continues. Ryther (1954) showed a low net rate of storage of C^{14} in aged cultures with high estimated gross photosynthesis. The system of small cells permits a high metabolism to continue in spite of low nutrients, because cycling is accelerated.

If this analogue theory is correct, one should be able to detect some sign of the very high gross photosynthesis and high respiration only in short-term experiments just after the onset of photosynthesis (net photosynthesis) and just after a sudden decrease of photosynthesis (respiration). With a square wave

of light input these pulses were recognizable in the brine system. Where gross photosynthesis may be declining in natural sunlight in the afternoon due to the gradual decrease of light and nutrients, the postsunset pulse may be less distinct.

An estimate of daytime respiration might be achieved by measuring the electron flow through the resistance (R) in a circuit such as that in Fig. 1, where the other metabolic measurements have been adjusted to correspond to actual data.

If the short-time constant pattern of diurnal metabolism is characteristic of large tropical and subtropical areas, such as the Sargasso Sea, then the present ideas about gross production in much of the ocean and in the biosphere as a whole must be modified upward considerably beyond the present estimated values. The large diurnal range in respiration may mask reciprocally a large gross photosynthesis. Thus the tropical oceans may be just as efficient in initially utilizing absorbed visible light energy in photosynthesis as other systems except that, with a general shortage of some nutrients, there is development of an evolutionary system that recycles the nutrients in a maximum way; the cycling rate may operate at a maximum during the daytime, while there is photosynthesis, and may almost shut down at night. Thus, the Sargasso Sea may undergo "nocturnal hibernation." In terms of net foods available to other trophic chains, this view of the tropical seas differs little from the present concept of these vast areas as deserts. However, in terms of efficiency in initial utilization of photons, total metabolism, nutrient cycling rate, and ability to compete with alternative possible ecosystems, this rapid-time constant theory implies that tropical seas are as productive in utilization of sunlight as other evolutionarily old, well-adapted, climax ecosystems. The relationships may be stated in another way: Nannoplankton cells at a high temperature and in a very inorganic medium where foods for heterotrophic assimilation are absent cannot store enough organic matter to last all night; therefore, their metabolism must of necessity approach zero for most of the night.

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