ological Potential and alogue Circuits for the Ecosystem

By HOWARD T. ODUM

Reprinted from AMERICAN SCIENTIST, Vol. 48, No. 1, March 1960

ECOLOGICAL POTENTIAL AND ANALOGUE CIRCUITS FOR THE ECOSYSTEM*

By HOWARD T. ODUM

The Ecosystem and the Ecomix

A PATCH of forest is a mysterious thing, growing, repairing, competing, holding itself against dispersion, oscillating in low entropy state, getting its daily quota of free energy from the sun. It is an ecosystem.

Understanding the basic nature of the ecosystem is a principal objective of ecology. Ecosystems are phenomena such as forests, deserts, lakes, reefs, lagoons, microcosm cultures, and polluted streams. They usually contain three kinds of processes, (*a*) photosynthesis, (*b*) respiration, and (*c*) circulation. Although extremely diverse, ecosystems have some basic structures and functional processes in common. To permit quantitative comparison on similar bases, a growing number of measures of general structure and function have been devised such as photosynthetic production, community metabolism, biomass, species variety, efficiencies, storage ratios, chlorophyll per area, assimilation ratio, turnover, etc. The time is now ripe for the further synthesis of the new data into generalized theorems of the ecosystem.

In ecosystems as in many other kinds of open systems, energy is supplied in concentrated form from the outside driving a sequence of branching energy flows, maintaining complex structure, recycling materials, and finally passing out from the system in a dispersed state of high entropy. The rate adjustments are set by natural selection which constitutes a fourth law of thermodynamics applicable to those open steady states which have self-reproduction and maintenance (Odum and Pinkerton, 1955).

The flow of energy in an ecosystem is represented by energy flow diagrams like that in Figure 1 (Odum, 1956). Organisms in an eco-

---

* These studies were aided by a grant from the National Science Foundation NSF G3978 on Ecological Microcosms.

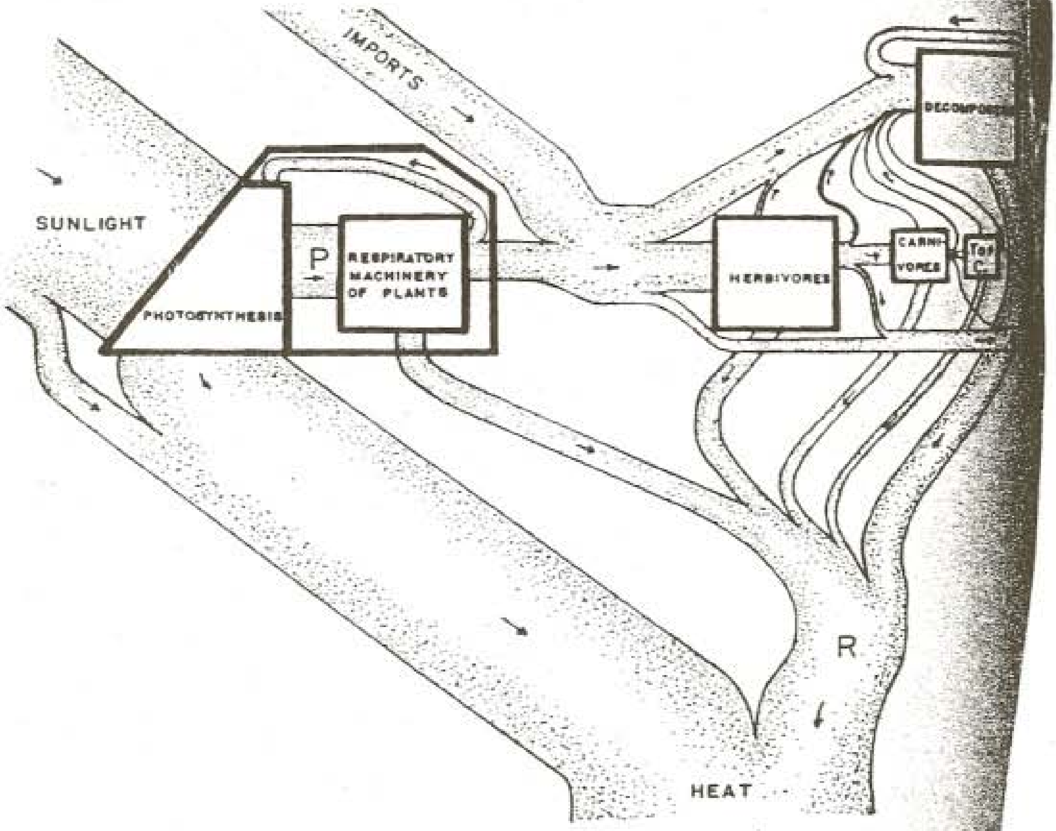

Fig. 1. Energy flow diagram for an ecosystem (Odum, 1956).

system in their food and energy roles participate at one of five relative positions in the flow circuit. These levels are usually called trophic levels as follows: primary photosynthetic producing plants, P; herbivore animals, H; carnivore animals, C; second order top carnivores, TC; and decomposer microorganisms and other components whose position is uncertain and for practical purposes must be lumped in a miscellaneous category pending elucidation of their exact role, D. These trophic levels are indicated in Figures 1, 2, and 3 by the boxes as labeled. Whereas the flow of energy is unidirectional towards dispersed, unavailable form according to the second law of thermodynamics, the materials such as carbon, nitrogen, phosphorus, and trace elements circulate in a cyclic manner being elevated into high energy combinations by plants, passing subsequently through a sequence of diminishing energy levels in the consumers. The cycle of the materials of an ecosystem can be represented by a diagram like that in Figure 2. Since the elemental ratios in the primary photosynthetic production tend to be similar to those in the respiratory-regenerator aspect of the ecosystem according to Redfield's principle

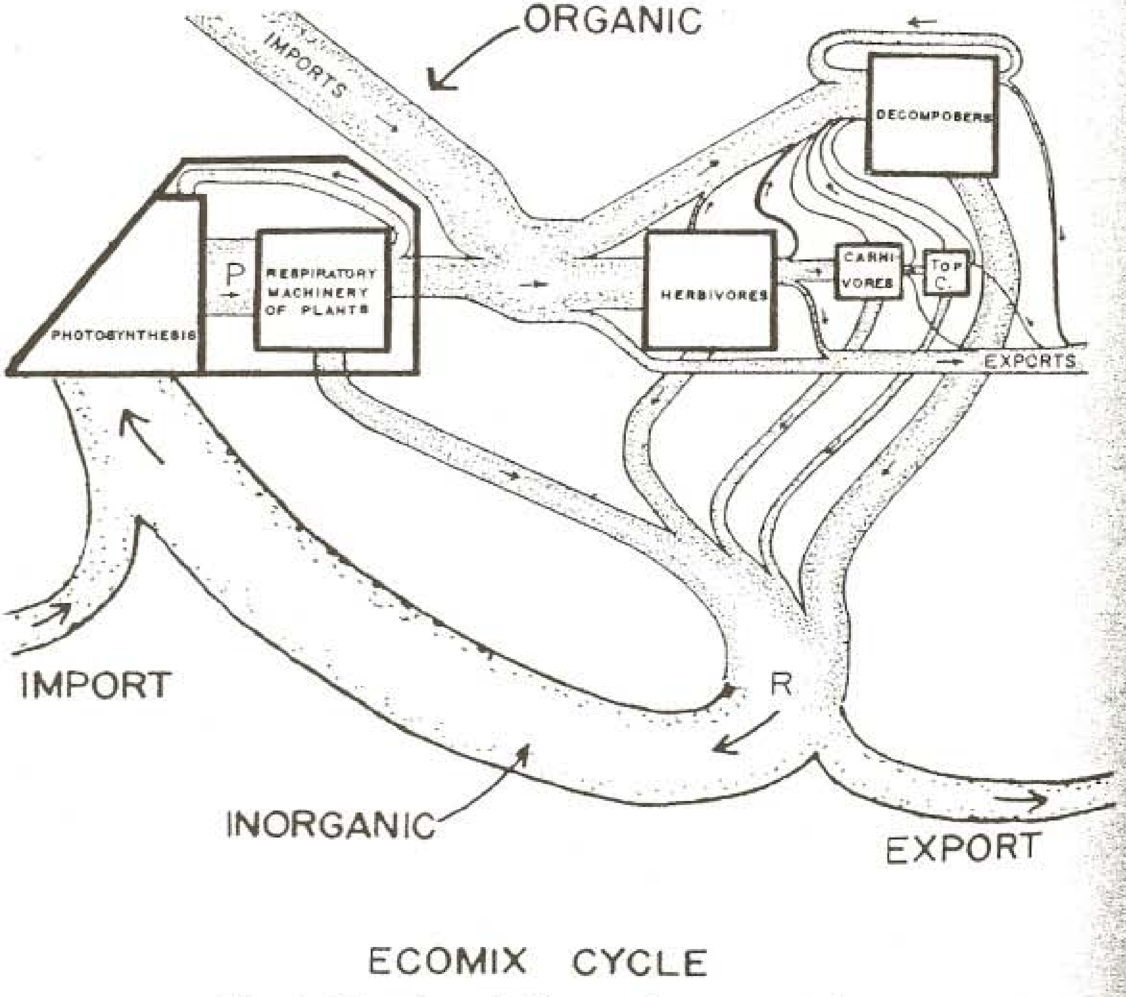

Fig. 2. Ecomix cycle diagram for an ecosystem.

(Redfield, 1934), one may consider the cycle of the raw materials as a group. The word ecomix is used in Figure 2 to represent the particular ratio of elemental substances being synthesized into biomass and subsequently released and recirculated. For example, the ratios of some of the elements in the ecomix of a planktonic system are indicated in the overall equation for the primary producers process:

1,300,000 Cal. radiant energy + 106 CO_2 + 90 H_2O + 16 NO_3 + 1 PO_4 plus mineral elements ⟶ 13,000 Cal. potential energy in 3258 gm protoplasm (106 C, 180 H, 45 0, 16 N, 1 P, 815 gm mineral ash) + 154 O_2 and 1,287,000 Cal. heat energy dispersed.

This and other explanations and examples of ecosystems may be found in an ecological text (Odum and Odum, 1959).

The Ecological Analogue of Ohm's Law

The familiar Ohm's law states that the flow of electrical current, A, is proportional to the driving voltage, V, with R, the resistance, a property of the circuit.

$$A = \frac{1}{R} V \qquad \text{(Ohm's Law)} \tag{1}$$

or, in an alternative form,

$$A = CV \tag{2}$$

where $C = 1/R$ is the conductivity.

In terms of steady state thermodynamics, Ohm's law is a special case of the more generalized theorem that the flux, J, is proportional to the driving thermodynamic force, X, with C the conductivity (Denbigh, 1951).

$$J = CX \tag{3}$$

Just as the product of voltage, V, and amperage, A, is power (wattage), so, in the general case, the product of thermodynamic force, X, and flux, J, is power, JX.

The ecosystem also has a flow of material under the driving influence of a thermodynamic force. The flux is the flow of food through a food chain circuit (Fig. 2) as expressed in units such as carbon per square meter of ecosystem area per unit of time. The force is some function of the concentration gradient of organic matter and biomass above and below the food circuit. A number of authors have related consumption to concentration. Jenny, Gessel, and Bingham (1949) have shown that the rate of organic decomposition by microorganisms in soil is proportional to the concentration of organic matter. A similar relationship is involved in the equation for the oxygen sag downstream from pollution outfall. Sinkoff, Geilker, and Rennerfelt (unpublished report obtainable from the Taft Environmental Health Center) use an analogue circuit for simulation of oxygen sag curves based on the principle of decomposition rate being dependent on the amount of organic matter. In comparing the ecosystem to the Ohm's law analogue, the consumption of living food as well as dead organic matter is considered to be dependent on the concentration of the food.

The validity of this application may be recognized when one breaks away from the habit of thinking that a fish or a bear catches food and thinks instead that accumulated food by its concentration practically forces food through the consumers. Any aggression by the fish is paid for by the food. When there are no consumers there is a state of high resistance. Usually, ecosystems rapidly develop circuits to drain reservoirs of organic free energy, often being self-organized to maintain suitable biomass structure for the purpose.

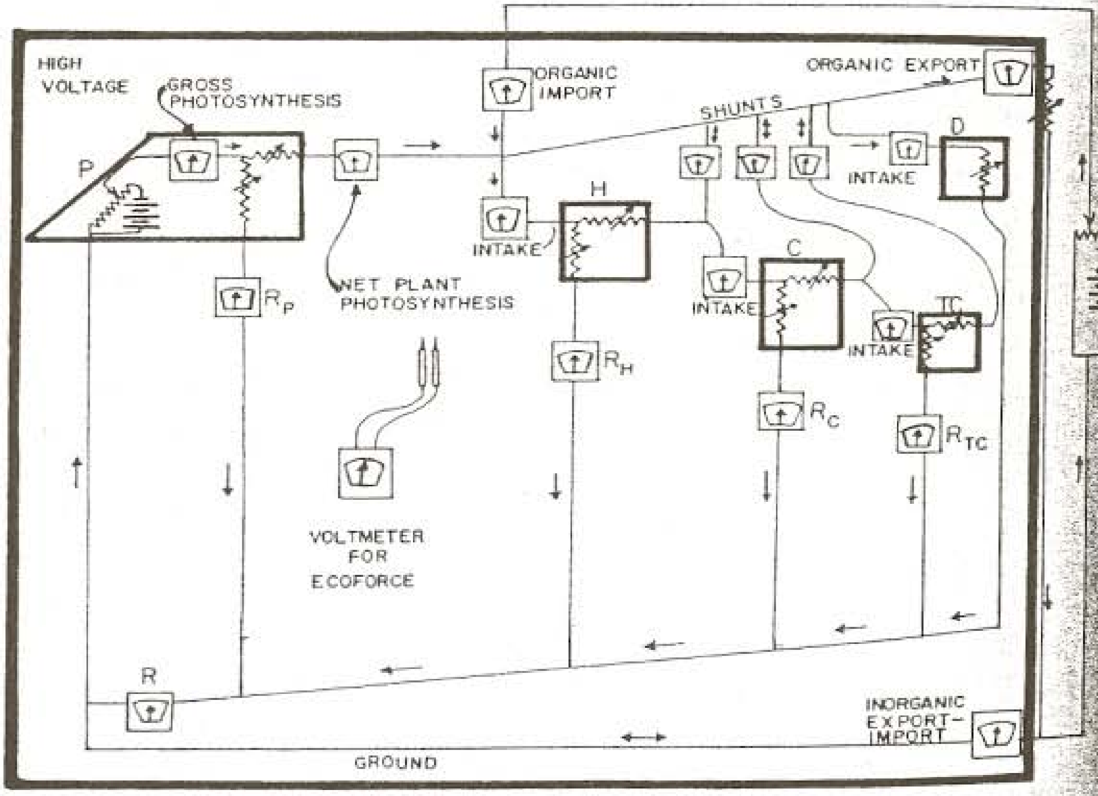

Fig. 3. Electrical analogue circuit for a steady state ecosystem like the one in Fig. The flow of electrons corresponds to the flow of carbon.

Thus we may write the equation for the force and flux in the ecosystem in the form of equations 1, 2 and 3 as follows:

$$J_e = C_e X_e \qquad (4)$$

where X_e is the thermodynamic force (ecoforce); J_e the ecoflux; and C_e the ecological conductivity of the food circuit. The application of equation (4) and the elucidation of the nature of the ecoforce follow in a subsequent section.

An Analogue Circuit for the Biogeochemical Cycle of the Ecosystem

Since the form of equation (4) relating ecoflux and ecoforce is the same as the form for Ohm's law, an electrical circuit can be constructed analogous to the flows of the ecomix in Figure 2. This has been done as diagrammed in Figure 3. Like the biological system in Figure 2, the electrical system in Figure 3 is an open steady state. Application of more complex analogue circuits with feedbacks, oscillations, and transient phenomena remain for the future.

In the electrical circuit of Figure 3 resistances are grouped at the locations of the producing and consuming populations. Batteries supply the concentrated energy representing the sun and the energy imported as organic matter from the outside. The various branching flows of food energy to consumers are presented with branching electrical wires. Variable resistances and switches permit the observer to set up various special situations and combinations. Milliammeters are placed in each circuit to permit rapid visual examination of the electrical flow which represents the flow of carbon and associated ecomix. As in the real ecosystem the energy is in the state of the flowing matter and is radiated from the computer as heat during passage from the high energy state of the battery to ground level. The amount of energy dispersed in any flow is readily measured by the product of the amperage and the voltage. A voltmeter with leads is available for measuring the voltage drop in any circuit adjustment.

Determination of the Ecoforce from Ecosystem Data Using the Electrical Analogue Circuit

Although approximate, fairly complete data now exist on rates of flux in circuits of real ecosystems. Data from one stable ecosystem, a fresh water stream, Silver Springs, Florida (Odum, 1957) available in the form of Figure 2, were put into the electrical analogue circuit (Figure 3) on a scale of 13.9 milliamperes per gm/M^2/year of carbon flow. The variable resistances were adjusted so that the rates of current flow were in scale with the average rates of flow of carbon estimated by various ecological means in the field. The voltage drops between the various parts of the ecosystem and the ground were then measured with the voltmeter. The results are included in Figure 4. The ecoforce, defined as a linear function of flux (equation 4), was thus measured directly from real data for an ecosystem using the electrical analogue circuit as a computation device.

Biomass Concentration, Ecoforce, and Ecopotential

As indicated previously, the flow of energy in a food chain circuit may be intuitively related to the concentration of food, just as the rates of reaction in simple chemical systems are related to the concentrations of reactants. However, the flow of energy between complex, self-reproducing entities organized within the ecosystem need not have, *a priori*, similarities to the chemical systems even though organic chemicals are involved in both.

The organic matter accumulated in the biomass of part of an ecosystem may be defined as ecopotential, E, equal to the free energy per unit carbon. This free energy, F, is the chemical free energy of the packages of biomass, prorated over the area of the ecosystem. Thus, ecopotential is a function of the concentration of biomass and organic matter.

The product of ecopotential and ecoflux has the dimensions of power.

$$EJ_e = \frac{\Delta F}{C}\frac{dC}{dt} \tag{5}$$

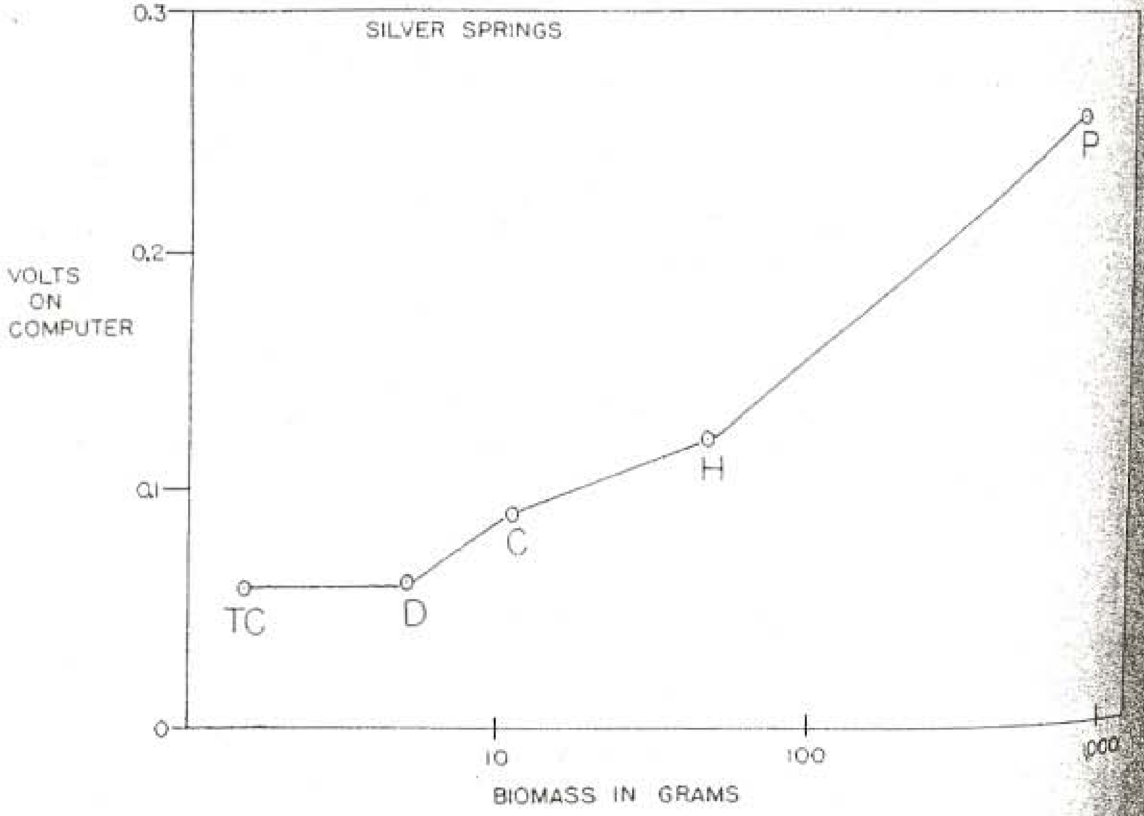

Fig. 4. Measured rates of metabolism of the organisms in the trophic levels of Silver Springs, Florida, were set in the circuit of Fig. 3 by adjusting the resistances. Then the voltages at this steady state were measured between the trophic level and ground. Since Ohm's law is a linear relationship, the voltages on the circuit are the ecoforces as defined in equation (4). The linearly defined ecoforce is some function of the organic food matter upstream from the trophic level. That is, the driving impetus to the metabolic circuits is some function of the concentration of food supply. At any point in the circuits the food supply is the standing concentration of biomass and other edible organic matter in the trophic level just above.

Measurements of the biomass concentration of organic matter in Silver Springs are available. In the graph of Fig. 4, the ecoforce is plotted as a function of the logarithm of biomass available to drive the flow. As one might predict from the basic similarity of ecological systems to chemical systems, the ecoforce is not the biomass concentration but may be a logarithmic function of it.

where E is ecopotential; J_e, ecoflux; ΔF, free energy change; C, carbon; and t, time.

Ecopotential is defined in energy units by equation (5); ecoforce was defined without specifying its dimensions except that it was linearly related to flux (equation 4). What is the relationship of ecopotential E and ecoforce X_e? In the case of Ohm's law, the potential and the force are identical. In the chemical flow systems, however, away from equilibrium, the potential is the logarithm of the force. The question arises as to the relationship of ecopotential and ecoforce in the ecosystem. Stating the question in another way, how is the flux related to the potential? Linearly? Logarithmically?

On the ordinate in Figure 4 are plotted the biomass concentrations from Silver Springs. On the abscissa are plotted the voltages from the electrical computer set for the average flux in Silver Springs. It is apparent that the relationship of biomass and voltage is not linear, but may be logarithmic. If the voltage of the computer represents the ecoforce defined linearly (equation 4) and the biomass concentration is a potential (equation 5), then ecopotential and ecoforce are not equal or linearly related. Many more such data need to be tested.

To avoid confusion it should be stated here that the concepts discussed here have nothing to do with the misnomer, biotic potential, which is not a potential in the energy sense but is a specific growth rate. Chapman's efforts (1928) to draw an analogy between Ohm's law and biotic potential are fallacious as can be recognized by dimensional analysis.

Hints About Ecosystems Derived from the Analogue Circuit

The construction and manipulation of the analogue is a powerful stimulant to the imagination concerning the behavior of ecosystems. The following are some suggestions from the analogue for experimental testing in the real ecosystems. The tests employed were made with the circuit in steady states resembling natural systems such as Silver Springs.

1. Competition exists when two circuits are in parallel.
2. Consumer animals compete with plant respiratory systems.
3. When unusual biomass and ecoforce distributions (potentials) are postulated, circuits reverse direction with food passing in unusual direction. For example, with large rates of import of organic matter, energy flows into the plants heterotrophically increasing plant respiration over its photosynthesis

6. If consumer respiration is increased, gross photosynthesis is also increased due to the lowered resistance.

7. Doubling the power supply doubles the metabolism at all levels.

8. Cutting off export increases metabolism of consumers.

9. Cutting off top carnivores does very little to the remainder of the energy flows.

10. Increasing import increases respiratory metabolism and diminishes gross photosynthesis.

11. Cutting out herbivores reduces photosynthesis and increases bacterial and plant respiration.

12. Higher trophic levels compete in part with the trophic level which it consumes.

13. A change in plant respiration has a major compensatory effect on the consumers.

14. A decrease in respiration increases the voltage (biomass concentration) upstream.

15. A short circuit is comparable to a forest fire.

ACKNOWLEDGMENTS

The author acknowledges the stimulation of theoretical discussions with Mr. Robert Beyers and Mr. Ronald Wilson of the Institute of Marine Science and with Dr. E. P. Odum, Dr. J. Olson, Dr. F. Golley, Dr. A. Smalley, and Dr. E. Kuenzler, participants in the 1959 Ecological Society Symposium on Energy Flow.

REFERENCES

CHAPMAN, R. N. 1928. The quantitative analysis of environmental factors. *Ecology, 9,* 111–122.

DENBIGH, K. G. 1951. Thermodynamics of the steady state. Methuen.

JENNY, H., S. P. GESSEL, and F. T. BINGHAM. 1959. Comparative study of decomposition rates of organic matter in temperate and tropical regions. *Soil Science, 68,* 419–432.

ODUM, E. P. with collaboration of H. T. ODUM. 1959. Fundamentals of Ecology. Saunders, Philadelphia.

ODUM, H. T. 1956. Primary production in flowing waters. *Limnolog. and Oceanogr., 1,* 102–117.

——— 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr., 27,* 55–112.

ODUM, H. T., and R. C. PINKERTON. 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *Amer. Sci., 43,* 331–343.

REDFIELD, A. C. 1934. On the proportions of organic derivations in sea water and their relation to the composition of plankton, pp. 176–192 in James Johnstone Memorial Volume, Liverpool Univ. Press, 348 pp.