Primary Productivity of the Biosphere

edited by Helmut Lieth
and Robert H. Whittaker

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Preface

The period since World War II, and especially the last decade influenced by the International Biological Program, has seen enormous growth in research on the function of ecosystems. The same period has seen an exponential rise in environmental problems including the capacity of the Earth to support man's population. The concern extends to man's effects on the "biosphere"—the film of living organisms on the Earth's surface that supports man. The common theme of ecologic research and environmental concerns is primary production—the binding of sunlight energy into organic matter by plants that supports all life. Many results from the IBP remain to be synthesized, but enough data are available from that program and other research to develop a convincing summary of the primary production of the biosphere—the purpose of this book.

The book had its origin in the parallel interests of the two editors and Gene E. Likens, which led them to prepare a symposium on the topic at the Second Biological Congress of the American Institute of Biological Sciences in Miami, Florida, October 24, 1971. Revisions of the papers presented at that symposium appear as Chapters 2, 8, 9, 10, and 15 in this book. We have added other chapters that complement this core; these include discussion and evaluation of methods for measuring productivity and regional production, current findings on tropical productivity, and models of primary productivity. The book is directed toward the interests of a range of readers, from those seeking summaries of research techniques to those concerned with our synthesis of global production.

Several institutions and people have helped to complete this work in its present form. The chapters contributed or coauthored by Lieth and Sharpe were supported in part by the Eastern Deciduous Forest Biome US-IBP. The chapters contributed by Whittaker and Hall were supported in part by Brookhaven National Laboratory; the contributions by Likens and Whittaker were supported in part by the National Science Foundation. During the final stage of editing this volume, one of the editors (HL) worked as guest researcher at the Nuclear Research Center (KFA) in Jülich, West Germany. We gratefully acknowledge the financial and logistic help received at the KFA through Prof. Dr. K. Wagener and his staff at the Institut für Physikalische Chemie. The index was compiled by Margot Lieth and Cyndi Grossman. We thank them both for their assistance. We gladly give credit to the staff of Springer-Verlag New York for excellent assistance in improving the book.

We hope this book will be of value for its characterization of the biosphere as a productive system. We are not confident of man's ability to control the future of the world or even his own existence. Nevertheless, we should be gratified if a focal point of the book—the net primary production of the biosphere—is one day seen as a figure of real significance to man. If in the future man's population and industry are stabilized, then to biosphere production as a steady-state flow of biological energy in the world will be related two other steady-state flows—of food energy from the biosphere to man and of industrial energy—that will support a human world society living in a durable balance with its environment.

Helmut Lieth
Robert H. Whittaker

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Part 1

Introduction

PREAMBLE

The last decades of biologic, and especially ecologic, research have made it clear that

1. The notion that man's population and wealth can increase without limit is self-deception and an invitation to self-destruction

2. The unregulated increase of the human population beyond the world's sustainable carrying capacity must be considered a moral crime

3. The relentless increase in the gross national products of the industrial nations, at the expense of the world population, must be considered a social crime

4. The reckless exploitation of our fossil fuel sources for short-term profit and growth, rather than careful planning for a reasonable use for a long-term future, is a crime against our own children

Helmut Lieth

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Scope and Purpose of This Volume

Robert H. Whittaker, Gene E. Likens, and Helmut Lieth

Some commonplace ideas of our time are that the surface of the earth is occupied by a film of living organisms, the "biosphere"; that the life of man and all other heterotrophic organisms is dependent on the primary production of the biosphere; and that the growth of man's population and industry affects the biosphere with increasing pressures, particularly those of harvest and chemical influence. These ideas are familiar, but some of the quantitative characteristics of the biosphere and man's relationship to it are not. Only in the last decade have sufficient data become available so that productive dimensions of the biosphere can be characterized by something better than educated guesses. Only in the last two or three decades has the unstable character of man's relationship to the biosphere become apparent to more than a small circle of scholars.

The word biosphere is used to mean either the global film of organisms or the surface environments of the world in which these organisms live and with which they interact (Hutchinson, 1970). This volume refers to "biosphere" in the first sense and expresses the second meaning as the "ecosphere" (Cole, 1958). The basis of all biosphere function is *primary productivity*, the creation by photosynthetic plants of organic matter incorporating sunlight energy. (This volume does not deal with the much smaller contribution of chemosynthetic autotrophic organisms.) The purpose of this volume is to synthesize current knowledge of world primary productivity in terms of methods of measurement, environmental determinants, the quantities for different communities and for the biosphere as a whole, the relationship to other biosphere characteristics, and the implications for man.

KEYWORDS: Primary productivity; ecology; phytogeography; biosphere.

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Our concern centers on *net* primary productivity, which is that part of the total or gross primary productivity of photosynthetic plants that remains after some of this material is used in the respiration of those plants. The remaining portion, net productivity, is available for harvest by animals and for reduction by saprobes. Net primary productivity provides the energetic and material basis for the life of all organisms besides the plants themselves. Net primary *productivity* is most commonly measured as dry organic matter synthesized per unit area of the Earth's surface per unit time, and is expressed as grams per square meter per year ($g/m^2/year \times 8.92 = lb/acre/year$).[1] Net *production* of ecosystem types in the world is expressed as metric tons ($t = 10^6$ g) of dry matter per year (metric tons $\times$ 1.1023 = English short tons). *Biomass* is the dry matter of living organisms present at a given time per unit of the Earth's surface, and may be expressed as kilograms per square meter ($kg/m^2 \times 10 = t/ha$, $\times 8922 = lb/acre$). Productivity may also be expressed as grams of carbon or calories of energy in the dry matter formed per unit area and time. The relationship of carbon to dry matter is variable, but 2.2 is a reasonable average by which carbon production may be multiplied to obtain dry matter. The energy content of plant biomass (in kilocalories per dry gram of tissue) is also variable, with a world average of about 4.25 for land plants, but with values around 4.9 for plankton and coniferous forest (see Table 7–2).

One of the purposes of this book is to summarize available data into an estimate of the world's total net primary production, for which we obtain 172×10^9 t/year. The pattern of production relationships in different kinds of communities that underlies this value has some complexity. In the three realms, the land, oceans, and freshwaters, net primary productivities range downward from 2000 to 3000 $g/m^2/year$ or more to near zero in desert conditions. Great contrasts in productivity are determined by water availability on land and nutrient availability in fresh and salt water, whereas temperature affects productivity everywhere. Over all, land communities are much more productive than are those of the oceans because land makes possible extensive community structure that retains nutrients and supports leaf surfaces. Marine plankton communities are far smaller in biomass, chlorophyll, and content of critical nutrients, as well as in the productivity that depends on these. Efficiency in use of light energy for productivity is generally correlated with primary productivity itself, but efficiency in productivity per unit chlorophyll is higher in marine plankton than it is in much more productive forests. Fractions of gross primary productivity spent in plant respiration vary with temperature and community biomass from 75% in tropical rain forest to probably 20–30% in some plankton communities. The energy content of plant biomass from different land communities varies in a

[1] As a way of expressing productivity we prefer $g/m^2/year$ for its direct translation into English as grams per meter square per year, and in particular prefer it to the cumbersome $g \cdot m^{-2} \cdot year^{-1}$. The $g/m^2/year$ form is potentially ambiguous, since it is possible to interpret it so that the year would go into the numerator. We have never encountered anyone who has thus misinterpreted it and doubt that the potential ambiguity is a real problem, but $g/m^2/year$ should of course be interpreted as $g/(m^2 \cdot year)$ or $(g/m^2)/year$.

definite pattern, from low values in tropical rain forest to high values in boreal forest.

At the moment it seems that man will not be able to restrain the growth of his population and industry before serious damage is done to the biosphere. If he is to do so, he must set limits on himself and plan for wise long-term use and conservation of the biosphere, based on knowledge of its characteristics. This book contributes to the understanding of the biosphere on which man's life and the healthfulness and attractiveness of his environment depends.

References

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Historical Survey of Primary Productivity Research

Helmut Lieth

From a recent paper on the history of the discovery of photosynthesis (Rabinovitch, 1971), it appears that many biologists equate photosynthesis with productivity and identify the raw materials of photosynthesis (water, carbon dioxide, and sunlight energy) as the direct controls of productivity. Photosynthesis and primary productivity are not so simply identical. Indeed, primary productivity—the actual energy bound into organic matter—is the product of photosynthesis. Yet primary productivity requires more than photosynthesis alone. The uptake and incorporation of inorganic nutrients into the diverse organic compounds of protoplasm are essential to the photosynthesizing organism. Temperatures govern annual productivity in various ways that do not result from temperature dependence of the photosynthetic process. On land, productivity is strongly affected by the availability of water, not primarily for use in the photosynthetic process itself, but to replace the water lost through the stomata that are open to allow carbon dioxide uptake.

This chapter compiles the key sources in the historical understanding of plant productivity as distinguished from photosynthesis. These include the gradual assessment of the global amounts and, to a limited degree, the understanding of the importance of primary productivity for man and environment.

In this history there are at least three major periods: (1) before Liebig, (2) from Liebig to the International Biological Program (IBP), and (3) the IBP and its consequences. Let us follow this sequence to see how the modern viewpoints and methods have developed.

KEYWORDS: Primary productivity; history; ecology.
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From Aristotle to Liebig

384–322 B.C. Aristotle taught that soil, in a manner comparable to that of the intestinal tract of animals, provides predigested food for the plants to take up through their roots. Thus he rightly emphasized the relationship between plant and soil while wrongly interpreting plant nutrition with an idea that was held generally for 1800 years.

1450 A.D. Nicolai de Cusa expressed the almost revolutionary idea that "the water thickens within the soil, sucks off soil substances and becomes then condensed to herb by the action of the sun."

A reading of the entire paper "Ydiote de staticis experimentis" (the Ydiote here meant is layman, most likely a practitioner with high technical skill) in Nicolaus de Cusa (Cusanus) *Werke* (1967) gives the impression that the "agricultural engineers" of his time held this plant–water relationship as a general consensus. Nicolai's view emphasized this relationship between plant and water. This paper appears to be the design for van Helmont's experiment about 150 years later.

ca. 1600 (1577–1644) van Helmont, besides performing odd experiments to find methods of obtaining mice from junk and sawdust, did one rather intelligent experiment. He grew a willow twig weighing 5 lb in a large clay pot containing 300 lb of soil, and irrigated it with rainwater. After 5 years, he harvested a willow tree of 164 lb of wood with a loss of only 2 oz of soil. van Helmont concluded from this that water was condensed to form plants.

1772–1777 or 1779 Priestley, Scheele, and Ingenhousz were the first to discuss the interaction between plants and air. They spoke about "melioration" and the "spoiling" of the air by plants in light or darkness.

1804 de Saussure studied the gas exchange of plants and gave the correct equation for photosynthesis:

$$\text{Carbon dioxide} + \text{water} = \text{plant matter} + \text{oxygen}$$

Following Rabinovitch's (1971) manner of indicating persons whose work led up to the primary production equation (not the photosynthetic equation), we have added the names of those who were instrumental in first evaluating the importance or necessity or both of each of the elements. Entries from Rabinovitch are in parentheses; our entries are in brackets [ ].

CO_2	+	H_2O	+	light	+	inorganic nutrients
(Senebier) [*Priestley–Scheele*]		*(de Saussure)* [*van Helmont*]		*(Ingenhousz)*		[*Liebig*]

YIELD

=	Oxygen	+	organic matter	+	chemical energy
	(Priestley)		*(Ingenhousz)* [*van Helmont*]		*(Mayer)* [*Boltzmann*]

Following the development of this equation, plant production was subjected to widespread, serious investigation, although not on the scale of present-day studies. The newly founded Colleges of Agriculture and Forestry dealt with various aspects of such questions.

From Liebig to the IBP

1840 The development of analytical chemistry enabled Liebig to show the importance of minerals for plant nutrition. He fought intensely against the generally accepted humus theory, which was based on the assumption that plants lived from organic matter only. While studying the relationship between dry-matter production and nutrient supply, Liebig formulated the well-known Law of the Minimum.

1850–1900 Plant chemistry uncovered the major relationships among plants, mineral nutrients, soil, water, and air. The importance of humus was investigated for all physical and chemical parameters significant in agriculture and forestry. The principles of matter cycles were widely discussed all over Europe; today it is difficult to determine who had the original ideas or evidence for primary productivity. These results were summarized in a few books that were cited frequently up to the early twentieth century (Boussingault, 1851; Liebig, 1862; and Ebermayer, 1876, 1882).

1862 Liebig was the first to think quantitatively about the impact of vegetation on the atmosphere. In 1862 he said, "If we think of the surface of the earth as being entirely covered with a green meadow yielding annually 5000 kg/ha, the total CO_2 content of the atmosphere would be used up within 21–22 years if the CO_2 were not replaced," ($230–240 \times 10^9$ metric tons CO_2 consumption per year, according to Liebig). This sentence marked the beginning of the geochemical treatment of productivity.

1882 Yield studies were easy to do with agricultural plants in laboratories and in the field, but forests presented special difficulties. The first dry-matter productivity figure for forests was not presented until 1882 when Ebermayer compared matter productivity of forests in Bavaria (from his own measurements) and field crops in France (data of Boussingault). Of course, the forests were more productive. His figures in kilograms per hectare of dry matter (= 10 times grams per square meter) are as follows:

Beech	Wood	3163 kg/ha		Potatoes	4080–4340 kg/ha
	Litter	3334		Clover	4200
	Total	6497		Wheat	4500
				Oats	4250
Spruce	Wood	3435 kg/ha			
	Litter	3007			
	Total	6442			
Pine	Wood	3233			
	Litter	3186			
	Total	6419			

These remained the key figures for about 50 years and were used again and again by geochemists in calculations of chemical elements in the biosphere. Forty years later, similar measurements were made by Boysen Jensen, Burger, Harper (see Lieth, 1962). Ebermayer presented the first estimation of world carbon binding of vegetation based on field measurements restricted to land areas. From his calculations for Bavaria he extrapolated that the annual consumption of CO_2 for the entire world was 90×10^9 t.

1900–1930 More than 60 years after Liebig's Law of Minimum, E. A. Mitscherlich developed this into the Law of Yield. This delay is rather surprising because the measurement of yield and dry-matter production had become very popular during Liebig's time. Mitscherlich's yield law is the first attempt to model productivity (Mitscherlich, 1954).

1908–1913 Figures similar to Ebermayer's (100×10^9 t) for CO_2 consumption were given by Arrhenius in 1908, and Cimacian in 1913, but neither gave additional biologic information (see Noddack and Komor, 1937).

1919 Schroeder (1919) provided the next major contribution to the knowledge of dry-matter production from the land. He based his calculations primarily upon Ebermayer's studies, but utilized more reliable information regarding the surface areas of forests,