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**Plant Metabolism**

Physiology and Biochemistry  
of Primary Metabolism

by Gerhard Richter



Georg Thieme Publishers Stuttgart

Gerhard Richter

# Plant Metabolism

Physiology and Biochemistry  
of Primary Metabolism

Translated by David J. Williams

101 Illustrations



Georg Thieme Publishers Stuttgart 1978

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Title of the original German edition:  
Stoffwechselphysiologie der Pflanzen

CIP-Kurztitelaufnahme der Deutschen Bibliothek

Richter, Gerhard:

Plant metabolism : physiology and biochemistry  
of primary metabolism. – 1. Aufl. – Stuttgart :  
Thieme, 1978.

Einheitssacht.: Stoffwechselphysiologie der  
Pflanzen (engl.)  
ISBN 3-13-549601-5

1st German edition 1969

2nd German edition 1971

3rd German edition 1976

1st Spanish edition 1972

1st Polish edition 1975

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© 1978 Georg Thieme Verlag, Herdweg 63, P.O.B. 732, D-7000 Stuttgart 1, FRG

Printed in Germany by Druckhaus Dörr, Inhaber Adam Götz, Ludwigsburg

ISBN 3 13 549601 5

5 4 3 2 1 0

## Preface

In recent years intensive experimental work has been done on various aspects of plant physiology, so that it is no easy task for the author of an introductory textbook of general botany to give a short review of the vast amount of new knowledge now available.

Metabolism is one of the most complex branches of plant physiology, and for years teachers and students have been conscious of the lack of an appropriate textbook. For students of biology, biochemistry, microbiology and pharmacy attendance at lectures is usually the only way to gain the necessary knowledge and acquaint oneself with the current state of research. The present textbook is intended to remedy this situation: it is based on lectures on plant physiology and the biochemistry of plant organisms.

For several reasons it seemed best to begin with a discussion of photosynthesis as the typical and central metabolic process of the green plant; this section is the longest in the book. From photosynthesis and chemosynthesis we proceed logically to those areas of reaction concerned with the winning of energy. A chapter on "Water and Ions in Metabolism" rounds off this section. Then follows a discussion of those transformations of matter which require energy from the areas mentioned and elements from the absorbed ions: biosynthesis of the cell's own chemical components. The book ends with a discussion of principles of regulation in plant metabolism. The material to be covered was selected in accordance with this general plan.

Special emphasis has been placed on two aspects of the subject: the close connection between biochemical functions and cellular structures, which is becoming more and more clearly established in molecular biology, and the significance of cross connections and contacts between at first sight unrelated areas of metabolism.

Experience has shown that the description of complicated biochemical processes of reaction is incomplete without a mention of the methods developed to explain and measure them. For this reason, short descriptions of methodological processes have been incorporated into the text wherever necessary. These will help the beginner to understand the more complicated subject matter and acquaint him with the most important aids in biochemical research. As students often have difficulty in grasping the principles and

peculiarities of biochemical reactions, the basics are dealt with in an introductory section.

Since the publication of the first German edition much new knowledge has come to light. For the English edition, each chapter has been thoroughly revised and new illustrations, diagrams and formulae have been incorporated wherever necessary.

I am grateful to my students and colleagues, especially Prof. W. Nultsch and Prof. G. Jacobi, for their helpful criticism and suggestions for improvement. Prof. H. Moor, Prof. G. Drews and Prof. W. Wehrmeyer provided the originals of the electronmicrographs, Dr. V. Hemleben read through the manuscript critically, Dr. W. Richter and Mrs. A. Fischer gave valuable assistance, and Mrs. M. Schober played a large part in preparing the manuscript for publication. My special thanks to all these, and to the publishers, Georg Thieme Verlag, for their splendid cooperation in the production of an English edition.

Hannover, May 1978

GERHARD RICHTER

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# Introduction

The term *metabolism* encompasses all the conversions of compounds which an organism or any of its cells uses to obtain chemical energy or to synthesize own complex molecular components. Generally, the conversions performed in these processes fulfill the criteria defining chemical reactions. They are almost always accelerated by *biocatalysts*, i.e. *enzymes*. Because of their close connection with living matter they are also termed "biochemical reactions".

The metabolism of the green plant is governed by *autotrophy*, thus differing from the metabolism of most other living organisms. By means of absorbed light energy plants are able to synthesize the organic substrate required for their metabolism from carbon dioxide, water and inorganic salts; oxygen is released in most cases. This primary process of transforming the energy of visible radiation into the energy of chemical bonds is called *photosynthesis*. The second form of autotrophy, *chemosynthesis*, is of less significance; by oxidation of inorganic compounds some organisms obtain sufficient energy to synthesize organic substrate from carbon dioxide and water. They are termed *chemoautotrophic* in contrast to the *photoautotrophic* organisms requiring light.

The metabolism of autotrophic plants stands in contrast to that of all other organisms, which are unable to build their organic substrate in this way. Most bacteria, the fungi, animals and man require exogenous complex organic compounds as vital substrate. These organisms are termed *heterotrophic* and their type of metabolism is called *heterotrophy*.

The existence of all heterotrophic organisms therefore depends on substances produced by autotrophic organisms. These provide all the various complex organic compounds which the heterotrophic organisms require for energy production and biosynthesis. Thus photosynthesis is of fundamental importance for life on earth since plants serve directly or indirectly as food and energy source for most other organisms. Figure 1 illustrates this interdependence. In living matter, organic compounds are subject to a typical cyclic turnover and are connected with oxygen, carbon dioxide and water as reaction partners. From the atmosphere green plants remove carbon dioxide and water which they use to build organic compounds by photosynthesis; oxygen is released. Heterotrophic organisms utilize

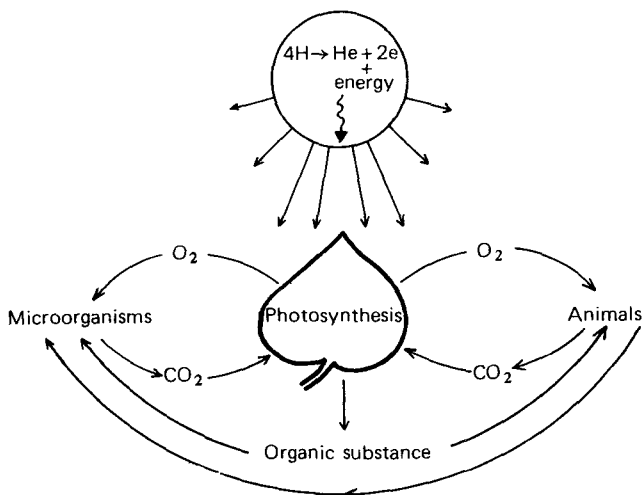


Fig. 1 The central position of photosynthesis in the turnover of living matter in nature.

this organic plant material consuming oxygen at the same time; the end products carbon dioxide and water return to the atmosphere, thus closing the cycle. Any disturbance of this equilibrium in carbon dioxide assimilation and production would have serious consequences for life on earth.

Not only organic material but also biologically utilizable energy passes along definite pathways within living matter. It originates from the radiant sunlight energy set free during the fusion of hydrogen nuclei to helium atoms at very high temperatures. This nuclear fusion releases electrons and relatively large quantities of energy in the form of gamma radiation:



The radiation undergoes a complex transformation process and eventually reaches the earth in the form of photons or quanta. Resembling a gigantic nuclear reactor, the sun provides the energy necessary for terrestrial life. Conversion of this energy into the chemical energy of metastable organic carbon compounds is effected via photosynthesis. This is the ultimate source from which green plants and, indirectly, heterotrophic organisms meet their energy requirements (see above).

The flow of energy within living matter is, however, associated with a continuous reduction in quality. The high energy content of

radiant energy is converted into the significantly lower one of an organic molecule and eventually into heat, a largely useless form of energy from a biological point of view. Unavoidable losses of energy, manifested as heat, occur in numerous chemical transformations. There is thus a natural downward gradient along which energy flows, which is irreversible; continuous "topping up" from the energy reserve of the sun is required.

From a thermodynamic point of view this dissipation of energy indicates transition of matter from a higher to a lower state of molecular order and a proportionate increase in *entropy*\*.

Apart from this crucial difference in the metabolism of autotrophic and heterotrophic organisms, there are common features which are often overlooked since the differences are more prominent. Firstly, those reactions which produce energy should be mentioned. Whether itself an independent organism or part of a more highly organized form of life, every cell combusts organic substrates to produce energy in a form which it can utilize. This complex process of *dis-similation* or *respiration* occurs in the same way in autotrophic and heterotrophic organisms. With consumption of oxygen, the fuel glucose is normally degraded to carbon dioxide and water (see below) in a process during which part of the energy released is trapped in "chemical energy equivalents" (Fig. 2). This enables the cell to perform the *biological work* vitally necessary for the maintenance of its integrity. Basically, there are three different forms of work: 1) *chemical* work; 2) uptake and transport of substances (*osmotic* work); and 3) *mechanical* work. We are mainly interested in the chemical work which encompasses the energy-consuming processes underlying the synthesis of cellular material. The most important components of the cell, the *macromolecules* such as proteins, nucleic acids, polysaccharides and also lipids, are formed from relatively small molecular building blocks mediated by specific enzymes. Macromolecular synthesis, giving rise to a net increase of cell substance, is a typical feature of growing cells and organisms.

However, biosynthesis also occurs in cells which are no longer dividing and which are fully differentiated; most of the constituents are subject to continuous renewal, i.e. there is a continuous dynamic turnover. Since degradation and synthesis proceed at equal rates, a "dynamic equilibrium" results, i.e. the cell substance does not in-

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\* *Entropy* is not only a measure of the state of molecular order, but also a measure of the dispersion of energy. Change to a disorganized state indicates an increase in entropy; establishment of a higher state of order indicates a decrease in entropy.

## 4 Introduction

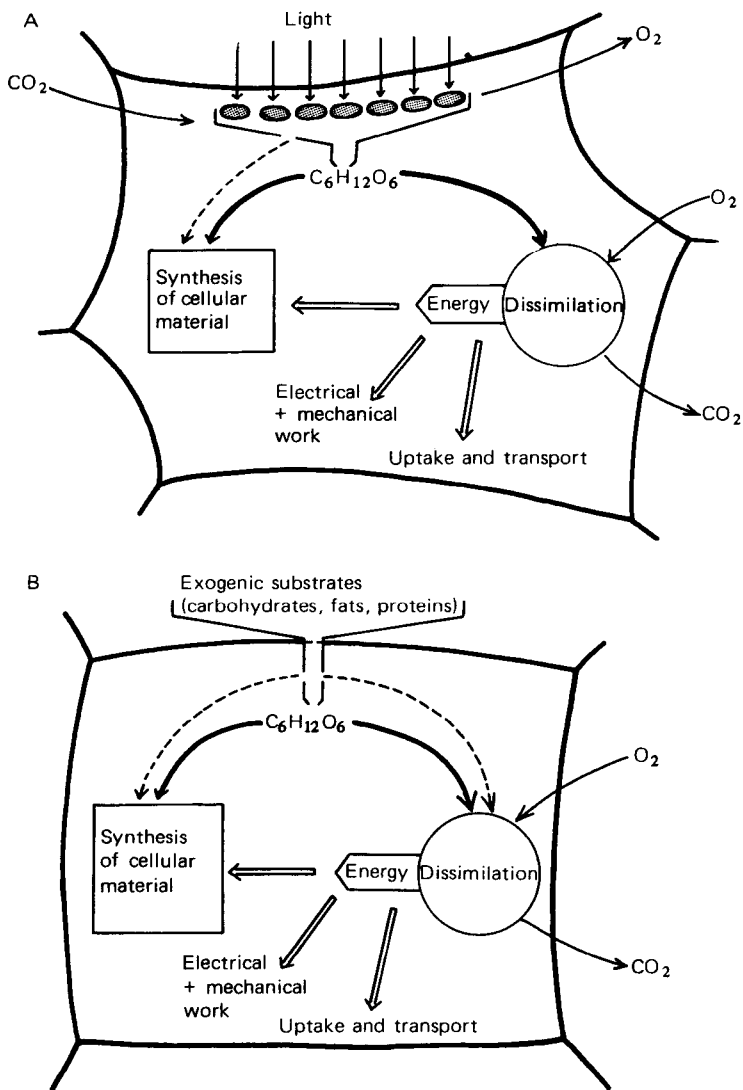


Fig. 2 Differences and mutual features in the metabolism of an autotrophic green plant cell and a heterotrophic animal cell (schematic).

crease in mass. The relative instability of cellular components emphasizes the dynamic element in metabolism.

Considering the synthesis and renewal of several macromolecular cellular components we come to another important feature. The chemical structure of these components enables them to store, transmit and also to express *information*. The information content of these macromolecules is responsible not only for maintaining the type specificity of a cell or organism during growth and multiplication but also for the precise synthesis of biologically active molecules, above all enzymes, the "construction plans" of which are laid down in the genetic material of each cell.

Dissimilation, the process yielding energy, was formerly distinguished as "operating metabolism" from the conversions concerned with the synthesis of cellular substance, the "building metabolism". This distinction is now largely outmoded; the two systems are so closely connected that boundary lines are indiscernible. Dissimilatory processes in autotrophic and heterotrophic organisms produce important precursors for synthesis, while synthetic processes provide substrates for energy production. The continuous renewal of cell components which involves most of the macromolecules and requires an input of energy, also indicates that the obviously contrasting processes of assimilation and dissimilation are closely interlocked.

The common features of autotrophy and heterotrophy are further exemplified by a "cellular division of labour". A close analogy can be seen when comparing a metabolically active cell with a chemical factory. The departments of the latter working together harmoniously under one roof find their counterparts in the various reaction spaces or *compartments* of a cell. In both cases, central regulation guarantees an equilibrium between the supply of raw materials and the output of end products. The production lines in the factory correspond to the reaction pathways of assimilation and dissimilation. Cellular division of labour is reflected in characteristic structures which are again comparable to specialized machines in a factory. The mitochondria are the organelles of energy production, the "power stations" of the cell. The pigment-bearing chloroplasts are the sites of photosynthesis. Protein biosynthesis takes place at the ribosomes. The regulatory and control center, the cell nucleus, contains the genetic material which provides the "construction plans" for the cell. The cytoplasmic membrane assumes control of the influx of products. Finally, the cytoplasm functions not only as a connecting medium between the organelles, but in its own right is an important reaction space in cellular metabolism.

# The Laws Governing Metabolic Reactions

The special characteristics of biochemical reactions must be known if complex metabolic events are to be understood. The following discussion is of an introductory nature and cannot replace an exhaustive study of the principles of organic chemistry and biochemistry, provided by the relevant literature.

## Chemical Equilibrium and "Steady State"

Knowledge of the laws governing chemical equilibrium and energetics is essential for the understanding of biochemical reactions. Between two reactants A and B a state is reached more or less quickly in which there is no longer any net change of the concentration ratio. The position of this chemical equilibrium is given by  $K = \frac{[B]}{[A]}$ , where "K" is the thermodynamic equilibrium constant, and the symbols in square brackets are the concentrations of reactant A and reaction product B respectively. Where there are several of these reactants or reaction products, the value of K is given by the product of the end products divided by the product of the reactants. Accordingly, for the conversion of A + B into C + D the equilibrium constant is

$$K = \frac{[C] \times [D]}{[A] \times [B]}.$$

The equilibrium constant K is closely related to another quantity, namely the free energy change ( $\Delta G$ ). This is the gain or loss of energy (in calories) during a particular chemical reaction. Energy is released when the reaction proceeds in the direction of the natural downward energy gradient, i.e. from a higher to a lower energy level. In such an "exergonic reaction",  $\Delta G$  has a negative sign since the decline of free energy is evaluated in the balance as a loss. In this case, K has a relatively high value; it signifies that the reaction  $A + B \rightleftharpoons C + D$  proceeds spontaneously and almost to completion. Finally, when equilibrium has been reached, much C + D but little A + B are present in the reaction mixture; the equilibrium has significantly "shifted to the right". When  $\Delta G = 0$ , the system does no longer release free energy.

A value of  $K$  below 1.0 indicates that there is little tendency for the reaction concerned to proceed spontaneously or approximately to completion. It requires an input of energy to proceed against the natural energy gradient, i.e. from a lower to a higher energy level. In such an "endergonic reaction",  $\Delta G$  has a positive sign; energy is invested in the system, the free energy change is positive.

The symbol " $\Delta G^\circ$ " designates the free energy change under "standard conditions": 1 mole/l of all reactants are dissolved in the reaction mixture; conversion of 1 mole in the reaction is taken as base value; the pH value is zero, i.e. the concentration or "activity" of  $H^\oplus$  equals 1; the temperature is 25 °C and the pressure 1 atmosphere. By means of this "standard quantity", the free energy change of a reaction can be calculated for all other concentrations of reactants as " $\Delta G$ ". The change in free energy of biochemical reactions is sometimes determined for the physiological pH value of 7.0; it is then designated " $\Delta G'$ " or " $\Delta G'^\circ$ ".

The laws governing chemical equilibrium apply only to *closed systems*. The latter are characterized in physicochemical terms by the fact that they do not exchange either matter or energy with their surroundings. They attain a true thermodynamic equilibrium, time and speed of reaction being without significance. However, a cell or an organism is not a closed system, but an *open system*; matter and energy are exchanged with the surroundings. A state of chemical equilibrium in the form set out above does not occur in the living cell because it would render the cell unable to obtain energy or carry out cellular work. Only a system which proceeds towards equilibrium has the capacity to release energy. Therefore in the living cell or organism, the situation is always such that equilibrium is continually approached but never reached, thus making a continuous supply of energy available for cellular work. Although the concentrations of the chemical components appear to be stationary, they are not usually in true thermodynamic equilibrium, but rather in a "steady state" in which the starting substances enter the system at the same rate as the end products leave it. In between there is a series of intermediate reactions during which the product of each preceding reaction is modified to yield the substrate for the next reaction.

Figure 3 attempts to illustrate these relationships schematically, although a profound explanation is still not available. The individual sub-systems and their components in dynamic steady state equilibrium are represented as vessels with an outflow using different symbols (circles, triangles, squares). The vessels form a descending sequence, and in each a dynamic equilibrium prevails since exactly as much starting material enters as end product leaves. Starting material drops into the uppermost vessel at the same speed with which the end product leaves the last vessel of the system. A photographic snapshot would give the (false) impression that the



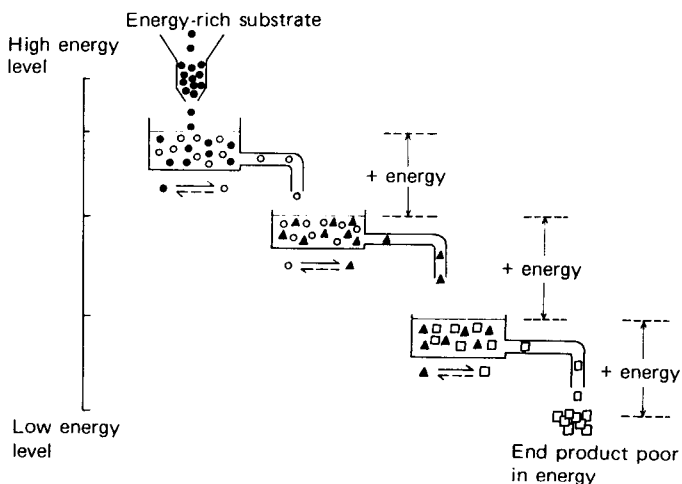


Fig. 3 Hypothetical model of a "dynamic steady state equilibrium" in a biochemical reaction chain. Details in the text.

concentration in each vessel is stationary; a moving film, however, would reveal the (true) state of a dynamic equilibrium.

The first vessel was placed at the highest level to show that, in the cell, starting substances with a relatively high energy content enter the system. Their stepwise degradation to an end product, poor in energy, corresponds to an overall exergonic reaction. This movement from a higher to a lower energy level is symbolized by the natural flow of fluid from one vessel to the next on a level below. The reaction chain proceeds spontaneously towards an energetically determined equilibrium which is, however, never reached. Energy is thereby continuously made available. The state of equilibrium arises when the input to the uppermost vessel ceases; the remaining vessels then run empty very quickly. For the cell or organism, such "running empty" means the end of energy production and consequently death. This catastrophe must be avoided by making available energy-rich substrate – autotrophically or heterotrophically – in order to maintain actively the established state of non-equilibrium. This is a basic attribute of living organisms. A number of important reaction sequences in cellular metabolism have been identified as "open" systems that exist in a dynamic steady state, e.g. the "respiratory chain" (for details see p. 241).

The complex steady state system does not, however, consist exclusively of exergonic reactions; they may be coupled or connected with endergonic processes which proceed by this mechanism (p. 19 f). This *energetic coupling* which plays an important role in me-