DAVID M. GREENBERG

Metabolic Pathways

VOLUME I

Metabolic Pathways

(Second Edition of *Chemical Pathways of Metabolism*)

EDITED BY

DAVID M. GREENBERG

Department of Biochemistry, School of Medicine
University of California, San Francisco, California

VOLUME I

1960

ACADEMIC PRESS · New York and London

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ACADEMIC PRESS INC.
111 FIFTH AVENUE
NEW YORK 3, N.Y.

United Kingdom Edition
Published by
ACADEMIC PRESS INC. (LONDON) LTD.
17 OLD QUEEN STREET, LONDON S.W. 1

Library of Congress Catalog Card Number 60-14866

PRINTED IN THE UNITED STATES OF AMERICA

CONTRIBUTORS

BERNARD AXELROD, *Department of Biochemistry, Purdue University, Lafayette, Indiana*

J. J. BURNS, *Laboratory of Chemical Pharmacology, National Heart Institute, National Institutes of Health, Bethesda, Maryland*

SIDNEY FLEISCHER, *Institute for Enzyme Research, University of Wisconsin, Madison, Wisconsin*

DAVID M. GIBSON, *Institute for Enzyme Research, University of Wisconsin, Madison, Wisconsin**

DAVID E. GREEN, *Institute for Enzyme Research, University of Wisconsin, Madison, Wisconsin*

W. Z. HASSID, *Department of Biochemistry, University of California, Berkeley, California*

LLOYD L. INGRAHAM, *Department of Biochemistry, University of California, Davis, California*

H. A. KREBS, *Medical Research Council Unit for Research in Cell Metabolism, Department of Biochemistry, University of Oxford, Oxford, England*

J. M. LOWENSTEIN, *Medical Research Council Unit for Research in Cell Metabolism, Department of Biochemistry, University of Oxford, Oxford, England*†

G. MACKINNEY, *Department of Food Science and Technology, University of California, Berkeley, California*

ARTHUR B. PARDEE, *Department of Biochemistry and Virus Laboratory, University of California, Berkeley, California*

R. J. ROSSITER, *Department of Biochemistry, University of Western Ontario, London, Canada*

LEO T. SAMUELS, *Department of Biochemistry, College of Medicine, University of Utah, Salt Lake City, Utah*

T. T. TCHEN, *Department of Chemistry, Wayne State University, Detroit, Michigan*

* Present address: Department of Biochemistry, Indiana University School of Medicine, Indianapolis 7, Indiana.

† Present address: Biochemistry Department, Brandeis University, Waltham 54, Massachusetts.

PREFACE

Knowledge of the metabolic processes of living organisms continues to accumulate at a gratifying pace. A wealth of new information has been acquired since the publication of the first edition of the work. Many missing details in the knowledge of particular intermediates and enzymes in established cycles have now been determined. New, hitherto unsuspected metabolic patterns have been discovered for many natural compounds. In many instances these represent alternate pathways to previously established metabolic cycles.

The last few years have seen the discovery of specific coenzyme functions for biotin and for vitamin B_{12}. Important progress has been made in the elucidation of the mechanisms of biosynthesis of the biological macromolecules primarily concerned with the maintenance of life processes, the proteins, and the nucleic acids.

These advances are discussed in this work. In addition separate chapters have been included on the metabolism of the carotenoids, vitamins, and coenzymes.

The purpose of this work remains, as in the first edition, to survey the existing knowledge of the chemical steps in the metabolism of the constituents of major importance in living organisms. In the selection of authors individuals have been chosen who are actively working in each of the areas covered and know the subject matter from personal day-today contact with it in the laboratory.

If one is led to wonder as to the reason for the change in title of these volumes, the answer is that the new title, "Metabolic Pathways" is strongly appealing for its brevity and connotations of content.

DAVID M. GREENBERG

University of California
School of Medicine
San Francisco, California
June, 1960

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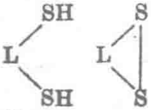
LIST OF COMMON ABBREVIATIONS AND SYMBOLS

AMP, GMP, IMP, UMP, CMP	The 5′-phosphates of ribosyl adenine, guanine, hypoxanthine, uracil, and cytosine
ADP	Adenosine diphosphate
ATP	Adenosine triphosphate
NMN	Nicotinamide mononucleotide
DPN_{ox}, DPN^+, DPN	Diphosphopyridine nucleotide (cozymase, coenzyme I)
DPN_{red}, DPNH	Reduced form of above
TPN_{ox}, TPN^+, TPN_{red}, TPNH	Triphosphopyridine nucleotide (coenzyme II)
FAD, $FADH_2$	Flavin adenine dinucleotide and its reduced form
CoA, CoASH	Coenzyme A
RSH	Sulfhydryl compounds
GSH, GSSG	Glutathione and its oxidized form
	Lipoic acid, thioctic acid
Kcal	Kilocalories
Kj	Kilojoules
Q_{O_2}, $Q_{acetate}$, etc.	Metabolic quotients expressed in μl metabolite/mg dry weight/hr
ΔF	Increment of free energy
ΔF^0	Standard free energy change
$\Delta F'$	Standard free energy change at pH 7
RNA	Ribonucleic acid
DNA	Deoxyribonucleic acid
P	Inorganic phosphate
PP	Inorganic pyrophosphate
PPP	Inorganic triphosphate
PLP	Pyridoxal phosphate
EDTA	Ethylenediamine tetraacetic acid

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Free Energy and Entropy in Metabolism

ARTHUR B. PARDEE
Department of Biochemistry and Virus Laboratory
University of California, Berkeley, California

AND

LLOYD L. INGRAHAM
Department of Biochemistry
University of California, Davis, California

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I. Introduction

The most useful concept that biochemists have acquired from thermodynamics is that of free energy. By considering the free energy change of a reaction one can tell whether it may proceed spontaneously or whether it must be "driven" by other reactions. Further, one can calculate the amount of energy given off by a reaction or required by it; and this is a most important feature of many reactions. From free energy data one can easily calculate equilibrium constants and electromotive forces.

In this chapter, an attempt will first be made to introduce the concept of free energy in a simple, descriptive way. The various methods of obtaining free energy data will be shown. Also, this section will provide relations between free energy and other quantities of direct interest, such as equilibrium constants, heats of reactions, and electromotive forces. The remainder of the chapter will be devoted to applications of thermodynamics which will serve to indicate areas of biochemistry in which such information is useful. The flow of energy through photosynthesis, assimilation into chemically stored forms such as starch, utilization of components with production of energy-rich phosphate compounds, and, finally, use for synthesis or work of various sorts will be mentioned. It is hoped that this presentation will provide a basis for understanding thermodynamic treatments in other chapters of this book and elsewhere in biochemistry.

Entropy changes are also of interest to biochemists, since such changes may give an insight into structural changes of the products relative to the reactants. A final section of this chapter will deal with applications of entropy in biochemistry.

Three types of information will be treated very briefly. First, little attempt will be made to relate free energy to other thermodynamic quantities. Many excellent books and articles on thermodynamics, some especially for biochemists, have appeared and may be recommended to those who are not familiar with the fundamental relations (*1–4*). Second, certain subjects such as applications of free energy in carbohydrate metabolism and protein synthesis are discussed in other chapters of this book, and therefore they will not be discussed at length in this chapter. Third, the eventual utilization of energy for work is outside the scope of this treatise.

II. Free Energy and Its Determination

A. The Nature of Free Energy

When we consider the energy changes involved in a reaction such as the oxidation of glucose or in a process like the absorption of light in photosynthesis, we note that chemical energy is given up as heat or that the energy of light is transformed into chemical energy. Such qualitative statements are not nearly as useful as quantitative information. Energy changes should be expressed quantitatively if they are to provide the maximum information regarding a reaction. The most useful way of expressing them is in terms of ΔF, the *free energy change* of the reaction. One may think of free energy changes in the following way: every compound may be considered to have a definite amount of free energy (F) stored in it under any set of conditions. When certain compounds (reactants) are converted into other compounds (products), the difference (Δ) in the free energies of products and reactants is released if the products have less free energy than the reactants, or energy must be put in if the opposite is the case. This difference, ΔF, is the free energy change of the reaction, per mole.

$$\Delta F = \text{free energy of products} - \text{free energy of reactants}$$

The point of greatest importance is that for the reaction to proceed spontaneously as written, without putting in outside energy (and at constant temperature and pressure), ΔF must be negative; that is, the products must possess less free energy than the reactants. One may say that reactions only go "down hill" energetically of their own accord—from compounds of higher to those of lower free energy. Processes that have a positive ΔF must be supplied with free energy greater than ΔF from another source if they are to proceed. They do not occur spontaneously. For example, formation of pyrophosphate from phosphate has a ΔF greater than 0 (+9,000 cal per mole). One could treat a solution of phosphate with catalysts like purified enzymes and the formation of pyrophosphate would not occur to an appreciable extent. However the reaction in the reverse direction can occur, since ΔF of hydrolysis of pyrophosphate is −9,000 cal. In the intermediate case, when ΔF of a reaction is 0, the reaction tends to go equally in both directions. The reactants and products are at equilibrium.

It might be helpful in discussing the nature of ΔF to mention its close relation to the equilibrium constant and the mass action law. In a reaction at equilibrium

$$A + B \rightleftharpoons C + D \qquad (1)$$

$(C)(D)/(A)(B)$ equals K, where (C), (D), (A), and (B) are concentrations and K is the equilibrium constant. When this ratio of products to reactants equals K the reaction is at equilibrium, when it is greater than K the reaction tends to go to the left, and when the ratio is less than K the reaction tends to go to the right; these correspond respectively to conditions of ΔF equal to 0, ΔF greater than 0, and ΔF less than 0.

It can be seen that the ΔF of a reaction must depend not only on the chemical structures of reactants and products but also on their concentrations, because the direction in which the reaction proceeds depends on these concentrations. It is not necessary to record ΔF for all possible concentrations since if ΔF is known for one set of conditions it can be calculated for others as described below. Therefore, ΔF is recorded when reactants and products are in certain standard conditions which are: liquids or solids, pure gases at 1 atmosphere, and substances in solution at 1 *M* concentration, at a definite temperature, usually 25°. Under these conditions concentrations are defined as equal to unity. This ΔF is written ΔF^0 and is called the standard free energy change. It is important not to use ΔF^0 in place of the ΔF calculated for the actual experimental conditions because ΔF^0 has no direct application and is the wrong value. For example, ΔF^0 of oxidation of $\frac{1}{2}$ N_2 to NO_3^- by O_2 equals +1780 cal, but ΔF under actual conditions in the bacterial cell is -7870 cal (*5*). An organism that operated under the standard conditions at which ΔF^0 is defined would fix little N_2. The method of calculating ΔF from ΔF^0 will be presented later in this chapter.

The second feature of interest is that ΔF is equal to the maximum energy "free" to do work obtainable from a reaction at constant temperature and pressure: for example, if a perfectly efficient man oxidized 1 mole of solid glucose with O_2 to CO_2 (gases at 1 atmosphere) and liquid water, he could do a maximum of 688,000 cal of work because ΔF^0 of the reaction equals $-688{,}000$ cal. ΔF does not include work done by any necessary expansion or contraction against external pressure during the reaction—in this case the volume change from O_2 and glucose to equivalent amounts of CO_2 and H_2O.

ΔF depends only on the products and reactants and not on the reaction pathway; for example, ΔF of the oxidation of glucose is the same whether the sugar is burned in a flame or metabolized in the body so long as the same initial and final conditions are obtained. No useful work is done in the first case and only heat is released, but ΔF of the reaction is the same, because it is equal to the maximum possible work obtainable and not to the actual work obtained.

The maximum heat that is released by a reaction at constant pressure is $-\Delta H$, and this is not necessarily the same as the maximum possible work, $-\Delta F$. As examples, a number of compounds including trichloroacetic acid and ammonium sulfate dissolve spontaneously in water so ΔF is negative; but the solution becomes cooler, and therefore at constant temperature heat would be absorbed, and ΔH must be positive. ΔF and ΔH may differ by plus or minus several thousand calories, as in the case of glycolysis, where ΔF is $-35{,}000$ cal and ΔH is $-24{,}000$ cal (*6*), one-third less. The difference between ΔH and ΔF is equal to $T\Delta S$ where ΔS is the difference in entropy of products and reactants.

$$\Delta H = \Delta F + T\Delta S \tag{2}$$

Entropy will be discussed in the final section of this chapter.

The free energy of a reaction is useful for determination of the direction of a reaction and the maximum energy yield, and in several other ways:

1. It can be used to calculate the equilibrium constant.
2. It can be used to calculate the electromotive force of an oxidation-reduction reaction.
3. It is useful in calculating other thermodynamic quantities.
4. By combining ΔF values of several reactions ΔF values of new reactions may be determined.
5. It provides a criterion for considering the possibility of occurrence of biochemical pathways.

Thermodynamics and a knowledge of the free energy of reactions is certainly useful and helpful but gives a far from complete picture of a biological situation. Although living systems must obey the laws of thermodynamics, these laws do not provide all types of information; hence, the outcome of any particular situation is difficult to predict from thermodynamic information alone. Thermodynamics does for a biochemist what a contour map without roads would do for a motorist. It tells him how far above or below him his destination lies, but it alone does not tell him whether there is a road he can follow—it tells him to where he cannot coast. Many reactions with negative ΔF do not proceed at a measurable rate; for example, gasoline is quite stable at room temperature in the presence of oxygen although its ΔF of oxidation is a large negative number. A negative ΔF is thus necessary for a reaction to occur but is not sufficient to predict whether it will occur. In other words, ΔF and the rate of a reaction are not related. This is because a molecule must obtain a certain amount of energy (activation energy) before it can react, independent of the possibility that the entire reaction may release energy. Enzymes are necessary to make biological reactions proceed at measurable rates. They do so by finding a pathway of lower elevation on the contour map. The fact that energy-rich compounds may be unreactive is very important because it means that the path of metabolism is not inflexibly one that yields the most energy at each step, but instead can lead to accumulation of compounds of high free energy content.

B. FREE ENERGY OF FORMATION

Free energy values usually are tabulated as standard free energies of formation of the compounds. This quantity is defined as the free energy change of the reaction in which the compound in its standard state is formed from the elements which compose it, in their standard states at the specified temperature. For example, the standard free energy of formation of solid glycine is −88,610 cal. This is the free energy change for the reaction:

$$O_2\text{ (1 atm)} + 2\text{ C (solid)} + \tfrac{1}{2}\text{ N}_2\text{ (1 atm)} + \tfrac{5}{2}\text{ H}_2\text{ (1 atm)} \rightarrow \text{CH}_2\text{NH}_2\text{COOH (solid)}$$

The free energies of formation of the elements are by this definition equal to zero. Tables of free energies and illustrations of the methods of calculation are available (*7–9*). Methods of determining ΔF will be presented in the remainder of this section.

C. DEPENDENCE OF ΔF ON CONCENTRATION

The free energy of a substance depends on concentration. Quantitatively, if C_1 and C_2 are two concentrations of a substance then F at C_1 is related to F at C_2 by the free energy change of the dilution. This work of dilution from C_1 to C_2 is equal to

$$RT \ln C_2/C_1 \tag{3}$$

where R is the gas constant (1.987 cal/mole/degree), T is the absolute temperature, and ln is logarithm to the base *e*. Rigorously, activities should be used in place of concentrations. (This refinement is not commonly used in biological work because the data are not sufficiently accurate and the activities are seldom known.) For example, F of $10^{-7}\ M\ \text{H}^+$ is equal to F of $1\ M\ \text{H}^+$ (defined as equal to 0) plus ΔF of the reaction in which 1 mole of $1\ M\ \text{H}^+$ is diluted to 1 mole of $10^{-7}\ M\ \text{H}^+$. At 37°,

$$\text{H}^+\ (1\ M) \rightarrow \text{H}^+\ (10^{-7}\ M)$$
$$\Delta F = 1410 \log 10^{-7}/1 = -9870 \text{ cal}$$

This means that 9870 cal would have to be used to compress 1 mole of H^+ from 10^7 liters into 1 liter of water (assuming maximal efficiency).

The logarithmic relation (Eq. 3) between ΔF and the concentration change has been presented without proof; but it may seem more reasonable if one considers the work required to compress a given amount of gas into successively smaller volumes, for example, from 100 ml to 10 ml and then from 10 ml to 1 ml. Although the volume change in the second step is only 1/10 that of the first, the total efforts are similar since the pressure becomes increasingly great as the volume decreases; and in fact the amount of work is theoretically the same in the two steps. The work would seem proportional to the per cent change in volume, and a logarithmic relation satisfies this requirement.

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