

Plant Physiology

A Treatise

Edited by

F. C. STEWARD

Volume I B

Plant Physiology

A T R E A T I S E

EDITED BY

F. C. STEWARD

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*Volume I B: Photosynthesis and
Chemosynthesis*

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Preface to Volume I

Since Volume II of this treatise actually preceded Volume I, it is desirable to recapitulate certain general aims and objectives of the whole work.

The aim of this treatise is to *say* what Plant Physiology is about and to do this in sufficient detail and with sufficient analysis of, and even extracts from, the ever expanding literature, so that each volume will be in large measure self-contained.

Plant physiologists will find that the treatment is sufficiently detailed to benefit their research in their own specialized fields and that the scope is broad enough to make reading of all portions of the work both stimulating and profitable. This treatise is, therefore, designed for the use of advanced and postgraduate students, teachers, research workers, and investigators in other fields of knowledge who need information about the present status of plant physiology. While such a synthesis of current knowledge is well justified by the great advances that have been made, especially in the last quarter of a century, its accomplishment requires the knowledge and mature experience of many authors who are aware of the trends in their often rapidly advancing fields of interest. Upon these authors, therefore, rests the quality and value of the work and to each the editor acknowledges his debt.

Although the treatise is now arranged in six volumes, each has been planned as a distinct unit and consists of a group of related chapters which, together, cover a major segment of the subject. Each chapter has been written by an authority in the field and analyzes the present status of its subject matter, giving pertinent references to the literature. The chief emphasis is on a synthesis of current knowledge, but consideration is also given to significant accomplishments of the past and, where possible, an insight into the problems of the future. Thus the reader may acquire an informed outlook on each topic.

While full advantage is taken of recent advances which accrue from the application of physical and biochemical techniques and the study of subcellular systems, the need to see the subject of plant physiology in terms of the morphology and organization of living plants is recognized throughout.

The treatise is intended not solely for use as a work of reference but is to be read by those who wish to obtain a reasoned analysis of the status and development of each subject which is discussed. Admittedly, and rightly, each chapter is affected by the author's own opinions, but, so far as possible in a work of this kind, an attempt has been made to achieve a measure of integration between the different chapters. Indexes make it possible for information to be traced by reference to an author's

name, to the plants used, or to the subject matter in question. For this volume the Index of Plant Names was prepared by Dr. W. J. Dress, and the Subject Index was compiled by Dr. H. Y. Mohan Ram. For this help the editor is grateful.

Volume I consists of two parts, A and B, each of which is complete with its own table of contents, separate pagination, indexes, etc. The consecutive numbering of Chapters 1 through 5, however, links these together as a single volume within the over-all plan of the treatise.

Even though Volume II has in fact preceded Volume I, it is still appropriate that the subject matter of Volume I should be considered first, for it concerns problems raised by the cellular and subcellular levels of organization within which physiological events occur, and it also deals with mechanisms by which cells store energy only to release it later for useful purposes.

While any of the subjects dealt with in Volume I could have been expanded beyond the limits of the present treatment, there were special reasons for the more extensive treatment of photosynthesis in Chapter 4 of Volume I B. The subject of photosynthesis, distinctive as it is of plants, has advanced so rapidly in recent years that an adequate treatment of all facets of the problem required a longer chapter. This plan was adopted even though it necessitated the division of Volume I A and I B into separate books. These parts now represent separate but closely related works on cells and cellular respiration in one unit (I A) and photosynthesis and chemosynthesis in the other (I B), and the hope is that the two parts will be the more useful because of their separate publication.

In both the treatment of cellular respiration, i.e. of energy release and utilization, and of photosynthesis, or energy storage, the attention is focused upon these physiological functions as they occur in cells. Other problems are to be raised at the level of organs or organisms, and these will be dealt with in Volume IV, along with other aspects of organic nutrition and of intermediary metabolism: this may account for some seeming gaps in the present treatment.

The separate acknowledgment to all those who have helped the authors and the Editor by permitting the inclusion of their published or unpublished material would be too great a task in a work of this kind. It should be understood, however, that both acknowledgment and thanks are conveyed by the form of citation in the text. The Editor wishes especially to acknowledge the helpful cooperation of the personnel of Academic Press.

F. C. STEWARD

Cornell University
November, 1959

PLANT PHYSIOLOGY

The Plan of the Treatise

The treatise is planned in three main sections, as follows:

Section on *Cell Physiology and Problems Relating to Water and Solutes*

The purpose of this section is to present the properties of cells, their energy relations (Volume I) and behavior toward water and solutes with the closely related problems of the movement of solutes within the plant body and the economy of water in plants (Volume II).

The underlying theme of Volumes I and II is the basis of plant physiology in cell physiology.

Section on *Nutrition and Metabolism*

In this section the detailed facts and knowledge of nutrition and metabolism are presented, first with reference to the need for, and utilization of, inorganic nutrients (Volume III), and second with respect to the processes of organic nutrition (Volume IV). The treatment of organic nutrition leads to a reconsideration of photosynthesis and respiration at the level of organs and organisms. Volume IV describes the intermediary metabolism of carbon and nitrogenous compounds and presents a brief comparison of plants in health and in disease.

The main theme of Volumes III and IV is the nutrition, organic and inorganic, of plants and the biochemical steps by which these processes are achieved.

Section on *Growth and Development*

The purpose of the last section is to present the problems of plant physiology as seen through the analysis of growth and development, mainly with reference to flowering plants. This entails (Volume V) a reappraisal of the main events of growth and development from the standpoint of morphology and leads to a consideration of growth of cells and of organs. Tropisms and the role of hormones and the effects of synthetic growth regulators are discussed. In Volume VI the attention is focused upon the quantitative analysis of growth and development, the physiology of reproduction, the development of fruits and seeds, the problems of dormancy and perennation. The role of environmental factors in the control of growth and development merits separate treatment. Finally the problems of growth and development are examined

from the standpoint of genetic control and from the interpretation of abnormal growth as seen in the formation of tumors. Throughout this treatment the controlling mechanisms of growth are evaluated.

Thus the last section of the work provides a synthesis of knowledge about plants since all their physiological processes converge upon growth and development.

The fulfillment of these objectives is possible only through the co-operation of many authors. The scope and treatment of individual chapters reflects the special interests of the contributors. While each volume is a complete unit, with its own table of contents and indexes, it is also an integral part of the whole plan.

Outline of the Plan

Section on *Cell Physiology and Problems Relating to Water and Solutes*

Volume I A. Cellular Organization and Respiration

Volume I B. Photosynthesis and Chemosynthesis

Volume II. Plants in Relation to Water and Solutes

Section on *Nutrition and Metabolism*

Volume III. Inorganic Nutrition of Plants

Volume IV. Organic Nutrition and Metabolism

Section on *Growth and Development*

Volume V. Analysis of Growth

Volume VI. The Physiology of Development

NOTE ON THE USE OF PLANT NAMES

The policy has been to identify by its scientific name, whenever possible, any plant mentioned by a vernacular name by the contributors to this work. In general, this has been done on the first occasion in each chapter when a vernacular name has been used. Particular care was taken to ensure the correct designation of plants mentioned in tables and figures which record actual observations. Sometimes, when reference has been made by an author to work done by others, it has not been possible to ascertain the exact identity of the plant material originally used, because the original workers did not identify their material except by generic or common name.

It should be unnecessary to state that the precise identification of plant material used in experimental work is as important for the enduring value of the work as the precise definition of any other variables in the work. "Warm" or "cold" would not usually be considered an acceptable substitute for a precisely stated temperature, nor could a general designation of "sugar" take the place of the precise molecular configuration of the substance used; "sunflower" and "*Helianthus*" are no more acceptable as plant names, considering how many diverse species are covered by either designation. Plant physiologists are becoming increasingly aware that different species of one genus (even different varieties or cultivars of one species) may differ in their physiological responses as well as in their external morphology, and that experimental plants should therefore be identified as precisely as possible if the observations made are to be verified by others.

On the assumption that such common names as lettuce and bean are well understood, it may appear pedantic to append the scientific names to them—but such an assumption cannot safely be made. Workers in the United States who use the unmodified word "bean" almost invariably are referring to some form of *Phaseolus vulgaris*; whereas in Britain *Vicia faba*, a plant of another genus entirely, might be implied. "Artichoke" is another such name that comes to mind, sometimes used for *Helianthus tuberosus* (properly, the Jerusalem artichoke), though the true artichoke is *Cynara scolymus*.

By the frequent interpolation of scientific names, consideration has also been given to the difficulties that any vernacular English name alone may present to a reader whose native tongue is not English. Even some American and most British botanists would be led into a misinterpretation of the identity of "yellow poplar," for instance, if this ver-

nacular American name were not supplemented by its scientific equivalent *Liriodendron tulipifera*, for this is not a species of *Populus* as might be expected, but a member of the quite unrelated magnolia family.

When reference has been made to the work of another investigator who, in his published papers, has used a plant name not now accepted by the nomenclatural authorities followed in the present work, that name ordinarily has been included in parentheses, as a synonym, immediately after the accepted name. In a few instances, when it seemed expedient to employ a plant name as it was used by an original author, even though that name is not now recognized as the valid one, the valid name, preceded by the sign =, has been supplied in parentheses: e.g., *Betula verrucosa* (= *B. pendula*). Synonyms have occasionally been added elsewhere also, as in the case of a plant known and frequently reported upon in the literature under more than one name: e.g., *Pseudotsuga menziesii* (*P. taxifolia*); species of *Elodea* (*Anacharis*).

Having adopted these conventions, their implementation rested first with each contributor to this work; but all outstanding problems of nomenclature have been referred to Dr. W. J. Dress of the Bailey Hortorium, Cornell University. The authorities for the nomenclature employed in this work have been Bailey's *Hortus Second* and Bailey's *Manual of Cultivated Plants* for cultivated plants. For bacteria Bergey's *Manual of Determinative Bacteriology*, for fungi Ainsworth and Bisbee's *Dictionary of the Fungi* have been used as reference sources; other names have been checked where necessary against Engler's *Syllabus der Pflanzenfamilien*. Recent taxonomic monographs and floras have been consulted where necessary. Dr. Dress' work in ensuring consistency and accuracy in the use of plant names is deeply appreciated.

THE EDITOR

CONTENTS OF VOLUMES I A AND II-VI

Volume I A. CELLULAR ORGANIZATION AND RESPIRATION

The Plant Cell and Its Inclusions—R. BROWN

Proteins, Enzymes, and the Mechanism of Enzyme Action—
BIRGIT VENNESLAND

Cellular Respiration—DAVID R. GODDARD and WALTER D. BONNER

Volume II. PLANTS IN RELATION TO WATER AND SOLUTES

Cell Membranes: Their Resistance to Penetration and Their Capacity
for Transport—RUNAR COLLANDER

Water Relations of Cells—T. A. BENNET-CLARK

The Water Relations to Stomatal Cells and the Mechanisms of Stomatal
Movement—O. V. S. HEATH

Plants in Relation to Inorganic Salts—F. C. STEWARD
and J. F. SUTCLIFFE

Translocation of Organic Solutes—C. A. SWANSON

Translocation of Inorganic Solutes—O. BIDDULPH

Transpiration and the Water Economy of Plants—PAUL J. KRAMER

Volume III. INORGANIC NUTRITION OF PLANTS

(Tentative Contents)

Historical: Mineral Nutrition in Soils and Solutions—C. BOULD and
E. J. HEWITT

The Essential Nutrient Elements: Requirements and Deficiencies—
E. J. HEWITT

Inorganic Nutrition of Microorganisms—D. J. D. NICHOLAS

Modes of Action of Essential Nutrient Elements—W. D. McELROY and
A. NASON

Nitrogen Fixation and Related Topics—A. I. VIRTANEN and J. K.
MIETTINEN

Microbial Activities in Soil as They Affect Plant Nutrition—J. H. QUASTEL

Volume IV. ORGANIC NUTRITION AND METABOLISM
(*Tentative Contents*)

Photosynthesis (Carbon Assimilation): Environmental and Nutritional Relationships—M. D. THOMAS

Organic Nutrition of Heterotrophic Plants: Carbohydrate Metabolism
—MARTIN GIBBS

Metabolism of Organic Acids—H. BEEVERS and MARY L. STILLER

Fat Metabolism—V. S. BUTT

Respiration of Organs and Organisms—E. W. YEMM

Metabolism of Organic Nitrogen Compounds—F. C. STEWARD and J. K. POLLARD

Comparative Physiology of Plants in Health and Disease—E. G. BOLLARD and R. E. F. MATTHEWS

Volume V. ANALYSIS OF GROWTH
(*Tentative Contents*)

Morphological Introduction to Growth and Development—R. H. WETMORE and TAYLOR STEEVES

Cell Growth and Division—R. BROWN

Growth in Organized and Unorganized Systems—H. E. STREET

Germination and the Growth of Roots—R. BROWN

Hormone Concepts in the Analysis of Growth—K. V. THIMANN

Tropisms and Tactic Responses—NIGEL BALL

Chemical Growth Regulators—R. L. WAIN

Volume VI. THE PHYSIOLOGY OF DEVELOPMENT
(*Tentative Contents*)

Quantitative Analysis of Growth and Development: Growth and Form
—F. J. RICHARDS

CONTENTS

| | |
|---|------|
| CONTRIBUTORS TO VOLUME I B | v |
| PREFACE TO VOLUME I | vii |
| THE PLAN OF THE TREATISE | ix |
| NOTE ON THE USE OF PLANT NAMES | xi |
| CONTENTS OF VOLUMES I A and II-VI | xiii |
| Preamble to Chapters 4 and 5 | xvi |

CHAPTER FOUR

| | |
|---|-----|
| Energy Storage: Photosynthesis <i>by</i> HANS GAFFRON | 3 |
| I. Introduction. | 4 |
| II. Materials and Methods | 22 |
| III. Chloroplast Structure and Constituents | 29 |
| IV. Chemistry and Photochemistry of the Chlorophyll Molecule <i>in Vitro</i> | 45 |
| V. Influence of External Factors on the Rate of Photosynthesis | 58 |
| VI. Absorption, Fluorescence, and Luminescence in Living Cells | 83 |
| VII. Photosynthesis in Flashing Light and the Photosynthetic Unit | 107 |
| VIII. The Storage of Energy and the Efficiency of Photosynthesis | 114 |
| IX. The Fixation and Reduction of Carbon Dioxide | 136 |
| X. Carbon Assimilation in Purple and Green Bacteria | 161 |
| XI. Hydrogenases in Bacteria and Adapted Algae | 175 |
| XII. Photosynthesis with Cell Extracts: Chloroplast Reactions | 194 |
| XIII. Energy Transfer by Active Phosphate in Photosynthesis | 205 |
| XIV. Effect of Poisons | 218 |
| XV. Transient Effects (Induction Periods) | 225 |
| XVI. Problems and Explanations | 237 |
| References | 247 |

CHAPTER FIVE

| | |
|---|-----|
| Chemosynthesis: The Energy Relations of Chemoautotrophic Or- ganisms <i>by</i> MARTIN GIBBS and JEROME A. SCHIFF | 279 |
| I. Introduction. | 279 |
| II. Thermodynamic Considerations | 280 |
| III. Chemical Transformation in the Assimilation of Sulfur and Nitrogen | 287 |
| IV. Chemosynthesis | 298 |
| V. Conclusion | 315 |
| References | 316 |
| Author Index | 321 |
| Index to Plant Names | 332 |
| Subject Index | 335 |

Physiology of Reproduction: Photoperiodism, Thermal Periodicity,
Vernalization—F. G. GREGORY and W. W. SCHWABE

Development of Fruits and Seeds: Rest Period, Dormancy, and Perennation—J. P. NITSCH

Environmental Factors in Regulation of Growth and Development:
Ecological Factors—F. E. WENT

Growth and Reproduction of Microorganisms—R. J. RAPER

Genetics and Development—A. M. SRB and H. H. SMITH

Abnormal Growth: The Tumor Problem—A. C. BRAUN

PREAMBLE TO CHAPTERS 4 AND 5

Chapters 4 and 5 should be considered together, for they deal with the questions which surround the acquisition of energy by plants and its storage in ultimately usable chemical forms. In these chapters the emphasis is placed upon the means by which the energy transfers are negotiated, since the cellular organization of the system in which they are mediated has already been described (Chapter 1, Volume IA). The great importance of photosynthesis in the over-all economy of nature justifies the particular attention here paid to this process as the main portion of Volume IA of the treatise. It is now dramatically evident that the hydrogen transfer from water, which occurs in green cells by photolysis, plays a key role in the ultimate reduction of carbon dioxide; whereas the recombination of hydrogen with oxygen to form water is an equally important event in the means by which the energy is released from the reduced and therefore energy-rich compounds. Whereas light is the source of the energy which is built into the compounds produced in photosynthesis, the necessary energy is donated by chemical means in chemosynthetic processes. Understanding of the energy storage in chemically usable forms in cells therefore requires a consideration of both photosynthesis (Chapter 4) and chemosynthetic (Chapter 5) processes.

CHAPTER FOUR

Energy Storage: Photosynthesis

HANS GAFFRON

| | |
|--|-----|
| I. Introduction | 4 |
| A. Photosynthesis—Definition and General Survey..... | 4 |
| B. Photosynthesis as a Complex Metabolic System..... | 10 |
| C. Photosynthesis as a Very Improbable Photochemical Reaction..... | 17 |
| II. Materials and Methods..... | 22 |
| A. Plant Material..... | 22 |
| B. Methods | 25 |
| III. Chloroplast Structure and Constituents..... | 29 |
| A. Structure of the Chloroplast..... | 29 |
| B. Chloroplast Constituents..... | 34 |
| C. Formation of Pigments..... | 40 |
| IV. Chemistry and Photochemistry of the Chlorophyll Molecule <i>in Vitro</i> | 45 |
| V. Influence of External Factors on the Rate of Photosynthesis..... | 58 |
| A. Light | 58 |
| B. Temperature | 66 |
| C. Carbon Dioxide Concentration..... | 66 |
| D. Water | 72 |
| E. Oxygen, Aerobic and Anaerobic Conditions..... | 72 |
| VI. Absorption, Fluorescence, and Luminescence in Living Cells..... | 83 |
| A. Absorption and Action Spectra <i>in Vivo</i> | 83 |
| B. Inactive Chlorophyll in Growing Cells..... | 88 |
| C. Specific Reactions of β -Carotene..... | 90 |
| D. Observing the Primary Process <i>in Vivo</i> | 91 |
| VII. Photosynthesis in Flashing Light and the Photosynthetic Unit..... | 107 |
| A. Flashing Light..... | 107 |
| B. The Photosynthetic Unit..... | 111 |
| VIII. The Storage of Energy and the Efficiency of Photosynthesis..... | 114 |
| A. Avoidable and Unavoidable Energy Losses..... | 121 |
| B. Difficulties Encountered in Determining Quantum Numbers..... | 122 |
| C. Oxygen Evolution..... | 127 |
| D. The Energetics of Photosynthesis..... | 130 |
| E. Quantum Numbers and Biochemical Mechanism..... | 133 |
| IX. The Fixation and Reduction of Carbon Dioxide..... | 136 |
| A. Enzymatic Carboxylations in Living Cells..... | 136 |
| B. The Use of Carbon Isotopes and the Discovery of Labeled Phosphoglyceric Acid..... | 138 |
| C. The Carboxylation Cycle..... | 145 |
| D. The Role of Light in the Carbon Cycle..... | 148 |
| E. The Carboxylation Enzyme..... | 158 |
| F. Other Carboxylations, Other Products..... | 159 |

| | |
|--|-----|
| X. Carbon Assimilation in Purple and Green Bacteria..... | 161 |
| A. Light Utilization and Emission..... | 165 |
| B. Products and Intermediates of Photoreduction..... | 168 |
| C. Fermentation and Respiration..... | 173 |
| XI. Hydrogenases in Bacteria and Adapted Algae..... | 175 |
| A. Photoreduction in Algae..... | 175 |
| B. The Oxyhydrogen Reaction and Chemosynthesis..... | 183 |
| C. The Photochemical Evolution of Hydrogen by Algae and Purple Bacteria..... | 185 |
| D. Nitrate, Nitrite, and Nitrogen Reduction in the Light..... | 188 |
| XII. Photosynthesis with Cell Extracts: Chloroplast Reactions..... | 194 |
| A. Reduction of Special Reagents..... | 195 |
| B. Reduction of Carbon Dioxide..... | 200 |
| C. Reduction of Coenzymes I and II..... | 204 |
| XIII. Energy Transfer by Active Phosphate in Photosynthesis..... | 205 |
| A. Energy-Rich Phosphate Bond ($\sim P$)..... | 205 |
| B. Light-Induced Phosphate Metabolism in Intact Cells..... | 209 |
| C. Phosphorylation by Chloroplasts and Chloroplast Fragments..... | 212 |
| XIV. Effect of Poisons..... | 218 |
| XV. Transient Effects (Induction Periods)..... | 225 |
| XVI. Problems and Explanations..... | 237 |
| A. Obsolete or Useless Hypotheses..... | 238 |
| B. Current Problems..... | 239 |
| Bibliographical Notes..... | 246 |
| References..... | 247 |

I. Introduction

A. PHOTOSYNTHESIS—DEFINITION AND GENERAL SURVEY

Photosynthesis—or the assimilation of carbon by plants with the aid of sunlight—is, strictly speaking, only a special chapter in the field of plant physiology. Yet, more than any other metabolic process in either plants or animals, it has aroused the interest and challenged the investigative skill of students in many branches of the natural sciences. This is easily understood if we consider that photosynthesis is the one reaction which maintains life in all its abundance on this planet.

With few minor exceptions, the carbon in natural organic matter originates from the carbon dioxide present in the air or dissolved in the oceans. It diffuses into the cells of land and water plants and, where these cells contain the green pigment, chlorophyll, carbon dioxide is transformed into carbohydrates, such as sucrose or starch which are primary nutrient materials for all things living. This transformation or synthesis occurs only in the light, and in the presence and with the participation of water. While carbon dioxide is being absorbed, the plants release an equivalent amount of oxygen gas. The light absorbed by chlorophyll is within that part of electromagnetic radiation which