PLANT PHYSIOLOGY

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SECOND EDITION—FOURTH PRINTING

D. VAN NOSTRAND COMPANY, INC.

PRINCETON, NEW JERSEY

TORONTO LONDON

NEW YORK

D. VAN NOSTRAND COMPANY, INC.

120 Alexander St., Princeton, New Jersey
257 Fourth Avenue, New York 10, New York
25 Hollinger Rd., Toronto 16, Canada
Macmillan & Co., Ltd., St. Martin's St., London, W.C. 2, England

All correspondence should be addressed to the principal office of the company at Princeton, N. J.

Published simultaneously in Canada by
D. Van Nostrand Company (Canada) Ltd.

Library of Congress Catalogue Card No. 52-9251

First Published, May 1939

Thirteen Reprintings

Second Edition, August 1952

Reprinted February 1954,

August 1955, August 1956

PRINTED IN THE UNITED STATES OF AMERICA

PREFACE

The widespread classroom and reference use of the first edition of this book has encouraged the authors to prepare this second edition. The revision has been a very thorough one and in many respects this second edition is virtually a new book.

As was true of the previous edition this book can be readily adapted to use with any introductory course in plant physiology based upon prerequisites of general botany and general chemistry. It can be used as the basis for a conventional recitation course or as a background source of information for student reading in connection with lecture-discussion courses. If only certain topics are selected for lecture or laboratory consideration, reading of the intervening chapters should help the student fit the classroom work into a coordinated picture of the science as a whole. Although the presentation is coordinated from chapter to chapter, the book has been planned so that more advanced phases of most topics can be skipped by omitting certain chapters and portions of chapters without materially disrupting the continuity of the discussion. This feature should make the book useful to those teachers who attempt to present a well-rounded course in plant physiology in one quarter or one semester.

While the content, organization and relative emphasis on various topics have undergone some obvious changes, the fundamental objectives of this second edition are virtually the same as those of the first. The authors have attempted to organize a discussion of the fundamental facts and principles of plant physiology which can be included between the covers of a volume of moderate dimensions. It has been our purpose to give some consideration to all topics which would be considered significant by the majority of plant physiologists. We have attempted to present a reasoned evaluation of the data rather than a mass of undigested facts and contradictory interpretations. Most of the discussion is based directly on data selected from the original literature, much of which is presented in tabular or graphical form. This approach is, we believe, consistent with the thesis that data are the source material from which all scientific concepts arise, yet it recognizes that facts alone may be a barrier to scientific progress unless fitted into a logical system of ideas. Students should grasp uncompromisingly the viewpoint that scientific knowledge is a structure of ideas derived from facts and observations.

Changes in the text from the previous edition are in content, emphasis, and organization. Modifications in content reflect principally advances in our knowledge of plant physiology over the last dozen years. Changes in emphasis and organization are based largely upon the judgments of the authors, often reinforced or tempered by suggestions from other teachers of plant physiology. Some condensation has been effected in the early discussion of basic physicochemical principles, because it is our impression that students are coming into plant physiology courses with a better background of such concepts than formerly. The chapters on various aspects of water relations have been somewhat abridged so that greater emphasis could be placed on metabolic processes and growth, those phases of plant physiology in which the most rapid advances have been made in recent years. A chapter on enzymes has been introduced just after the discussion of water relations, in order to catalyze an understanding of immediately following chapters on metabolic processes. This chapter replaces the chapter on digestion which in the first edition was given a much later position in the book. Also worthy of note is the shifting of the discussion of respiration to a position ahead of most discussion of metabolic processes. The increasing realization that respiration is the key to the synthetic as well as degradative processes of metabolism makes its earlier discussion desirable. The chapters on growth have undergone a considerable reorganization, one of the principal objectives of which has been the achievement of a sharper differentiation between vegetative and reproductive growth, which contrast just as greatly in their physiological as in their morphological aspects.

The authors are acutely aware that, for most of the students who will use this textbook, plant physiology is not an end in itself but a tool to the better understanding of the behavior of plants under natural or, at most, only partially controlled conditions. Recognition of this situation accounts for the essentially ecological viewpoint which underlies much of the discussion. The effects of various factors on different processes, relations between daily periodicities of plant processes and daily periodicities of environmental factors, and the bearing of seasonal cycles of environmental factors on seasonal patterns of plant behavior are consequently given a prominent place in the discussion. On the other hand, consideration of the mechanisms of processes, always ultimately needful in the explanation of ecological behavior, has also been quite comprehensive. Explanations of many process mechanisms require excursions into the domain of biochemistry which we have not hesitated to undertake whenever the level of interpretation which seemed desirable required it.

Although less emphasized than in the previous edition, considerable space is devoted to a review and extension of physicochemical principles with which the student of physiology should be familiar. Some of this discussion is essential for the interpretation of plant processes as such; some of it is essential for an understanding of the nature of the physical factors of the environment and the manner in which they influence plant processes. Likewise the structure of organs, tissues, and cells has been described at appropriate places as necessary background information. Structure and process are inseparable and an integrated picture of both is essential for a clear concept of any phase of the physiological activity of plants.

With only a few exceptions each chapter has appended to it a list of discussion questions. These lists are meant to be suggestive and it is recommended that each teacher supplement them with additional questions, of more or less similar purport, but adapted to the interests and background of his own student group. Most of the questions are of the "problem" type, and many of them have been deliberately chosen to extend the classroom discussion to applications which have not been considered in the text. Effective teaching in any science should not only lead to the acquisition by the student of the basic facts, principles, and viewpoints of that science, but should also train him in the use of that science in the interpretation of natural phenomena. The use of properly selected problems as a teaching device should aid the student in making use of the facts and principles of a science as well as learning them.

A large part of the manuscript of this edition has been read critically by Dr. H. T. Scofield of North Carolina State College and by Dr. C. A. Swanson of The Ohio State University. Certain chapters have likewise been critically read by Dr. G. W. Blaydes and Dr. R. C. Burrell of The Ohio State University, by Prof. T. C. Broyer of the University of California and by Dr. C. O. Miller of the University of Wisconsin. We are indebted to all of these readers for their constructive criticisms. Thanks are also due to Grace Townsend Meyer for checking most of the references. Those figures which have been taken from other sources are properly credited in the captions.

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Columbus, Ohio
Raleigh, N. C.
April, 1952

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I

THE FIELD OF PLANT PHYSIOLOGY

In an effort to understand the mechanism of a plant in its entirety, many separate phases of the dynamic activity of plants have been recognized and studied as individual processes. In attempting to interpret these individual processes and their interrelationships, the plant physiologist is confronted with many problems: What is the mechanism by which water, gases, and solutes enter a plant from its environment? How do such substances pass out of a plant into its surroundings? How are foods and other complex organic compounds synthesized in the plant? How are they utilized in the development and maintenance of plants as living systems? What transformations of energy occur within a plant, and what exchanges of energy take place between a plant and its environment? How are water and solutes transported from one part of a plant to another? How are new tissues constructed? How is the development of one organ or tissue coordinated with the development of other organs or tissues? Why does a plant produce only vegetative organs at certain stages in its life cycle and reproductive organs only at other stages? How are individual plant processes and the development of a plant as a whole influenced by environmental conditions? All of these problems and many other related or subsidiary ones lie within the province of the branch of science that is known as plant physiology.

For convenience, the study of plant life is subdivided into various branches such as physiology, morphology, anatomy, ecology, pathology, and genetics. Such a classification is necessarily more or less arbitrary. Neither physiology nor any other phase of plant life can be singled out for study without some consideration of plants from other viewpoints. A particularly intimate interrelationship exists between the structures and processes of plants. Every physiological process is conditioned by the anatomical arrangement of the tissues, and by the size, configuration, and other structural features of the cells in which it occurs. Furthermore, the coordinated development of cells and tissues, *i.e.*, of the plant itself, is a complex of physiological processes. Thus the sciences of plant physiology and plant anatomy merge in the study of plant growth.

Just as different species of plants differ in outward configuration and internal anatomy, so do they also differ in physiology. The world of plants includes a great number of very diverse kinds of organisms that range in size from simple bacterial cells a few microns long to the enormous redwoods of California. Their difference in size, although striking enough, is not as fundamental as another distinction which exists between redwoods and bacteria. The redwoods and all other green plants are able to manufacture their own food, while bacteria (with a very few exceptions) and all other non-green plants must obtain their nourishment from some outside source. The physiology of the green and the non-green plants is therefore basically unlike. This book is essentially a discussion of the physiology of the chlorophyllous (green) plants with the emphasis on the vascular green plants. The physiological processes of the bacteria and fungi have been considered only when they have a direct bearing on the physiology of the green plants.

In general the basic physiology of all vascular green plants is similar. This is not to say, however, that the processes occurring in one kind of green plant are always identical with those occurring in another. The physiology of a tomato plant differs from that of an oak tree in the same sense that the physiology of a horse is different from that of a cat. Many qualitative differences in metabolism are known to exist among plants. Most green plants, for example, synthesize starch, but many do not. Most of the physiological differences among species of green plants are quantitative rather than qualitative. All vascular green plants synthesize chlorophylls *a* and *b*, for example, but the proportions of these two pigments present differ considerably from one species to another. Similarly, under identical soil and climatic conditions, the rates of absorption of water by two kinds of plants may be very different. Even varieties of the same species may differ markedly in their physiological reactions to a given environmental complex. Under the same climatic and soil conditions, for example, some varieties of wheat are markedly cold resistant, while others are not.

The Relation of Physiology to the Physical Sciences.—Formerly the opinion was almost universal that living organisms owe their distinctive properties to the possession of subtle and unknown forces which are peculiar to "living matter." At the present time such "vitalistic" theories find very few advocates. The contrary and now widely held assumption is that living organisms operate in accordance with the same physicochemical principles that hold in the inanimate world. The complexity and elusiveness of living processes are not assumed to result from intangible, unknown varieties of energy, but to the intricateness of the interplay of recognizable physicochemical forces in the complex organized system of the protoplasm.

Adoption of this latter point of view has led to a widespread use of the tools of physics and chemistry in experimental work on plants, and to the interpretation of plant processes in terms of these two sciences. This has led to notable progress in our understanding of the physiology of plants and has permitted the analysis and expression of many physiological relations in quantitative terms.

A knowledge of certain fundamental principles of physics and chemistry is therefore essential to the understanding of physiological processes. For this reason several of the earlier and parts of some of the later chapters in this book are devoted to a brief exposition of certain underlying principles of the physical sciences with which a student of plant physiology should be familiar.

The Relation of Plant Physiology to the Agricultural Sciences.—Green plants are not only the ultimate source of all food but supply the raw materials for many of our basic industries. With the rise of modern industrial civilization both the quantities and kinds of plant products which we utilize have increased rather than decreased. In addition to foods some of the more important raw products obtained from plants are wood, textile fibers, pulp, rubber, vegetable oils, gums, and drugs. Even most of the so-called "synthetic products" of the chemist are not synthetic in the sense that they have been built up from simple inorganic compounds, but only insofar as they represent modifications of naturally occurring plant products.

An industrial civilization not only requires a wide variety of plant products but insists that these products meet certain standards of quality. The successful cultivation of plants has, therefore, become a highly skilled occupation, and the agricultural sciences are rapidly becoming a domain of the specialist. Success in controlling the activities of living plants cannot be achieved without some understanding of the processes which occur within them, and of the effects of environmental conditions upon these processes. The problems of the forester, the fruit grower, the cotton planter, the floriculturist, the grain farmer, and of all others who cultivate plants differ in detail, yet they all have a fundamental similarity in requiring an application of the principles of plant physiology for their solution.

Fundamental investigations in plant physiology have contributed in many ways to improved methods of propagating, cultivating, and harvesting economically important plants, and to methods of handling and storing many plant products. Furthermore, control of the fungous diseases and insect predators of plants often requires application of the principles of plant physiology. Much of the investigational work carried on by scientific agronomists, horticulturists, floriculturists, and foresters actually lies in the field of pure or applied plant physiology, although often it is not formally classed as such.

The last hundred years have witnessed the evolution of the agricultural sciences from largely empirical arts into the realm of applied sciences. More progress has been made in their improvement during this period than during all previous history. In substantial part this development of a scientific approach to the practice of agriculture has come as a result of advances in our knowledge of the physiology of plants.

Plant Physiology as a Science.—The origin of man's first conscious interest in plants long antedates recorded history. Agriculture had already become a highly developed art thousands of years before any experimental study of plant processes began. Consequently, there had grown up a vast body of traditional plant lore which passed orally from father to son, generation after generation. This practical knowledge of plants developed over many centuries as a result of countless, mostly involuntary, trial-and-error experiences and innumerable observations of plant behavior under all kinds of circumstances. Much of this mass of mingled facts and beliefs regarding plants is alive in the consciousness of the common man today. The closer he lives to the soil and the more familiar he is with traditional plant lore, the more they influence his thoughts and actions.

Many of these customarily accepted beliefs are essentially sound and most of them contain elements of truth. Others, however, are entirely erroneous, and not a few are tempered with superstitions, some of which have an unbroken lineage back to the days of witch-doctors and savagery. No reputable botanist has held for generations, for example, that plants obtain their food from the soil, yet this and many other fallacious beliefs are still widely entertained among the general population.

The value of practical information about plants should not be underrated, since its perpetuation in the mind of man permitted the development of agriculture to a high plane as a practical art before any widespread investigation of plants from a scientific point of view was undertaken. Nevertheless, traditional plant lore frequently is not only inadequate, but is riddled with misconceptions, and often suffers from points of view which are inherently stultifying to the acquisition of further knowledge.

The layman, for example, often personifies plants in an attempt to explain their behavior. Man has desires and foresight, and it is often assumed, either consciously or tacitly, that plants are similarly endowed. To many, for example, the statement that "roots grow downward in search of water," or that "stems grow upward in order to reach the light" are accepted as adequate "explanations" of plant behavior. Man's knowledge that water and light are essential to plants is not evidence that plants are similarly aware of these facts. To assume that plants realize their needs and are able to act in conformity with their requirements is equivalent to crediting them with a high order of intelligence. Explanations of plant behavior are commonly encountered in which purposeful action on the part of plants is tacitly or deliberately implied, although there is no justification for the adoption of such a point of view.

Furthermore, the layman seldom pursues his quest for information about plants beyond the stage of observation, while the scientist frequently does. Observation has suggested, for example, that light is necessary for the continued existence of plants. To one who is scientifically minded, either by instinct or training, the obvious next step is to test this postulate experimentally. If the suggested hypothesis is substantiated by experiment it is tentatively accepted as a theory. Theories such as those proposed in explanation of the processes or reactions of plants, together with the experimental results which are considered to support them, are usually published in a scientific journal or monograph and thus exposed to evaluation and further experimental testing by other scientists.

Continued experimentation may lead to substantiation, rejection, or modification of the theory as originally proposed. Modification would undoubtedly be the fate of the hypothesis used as an example, since sooner or later some investigator would find that non-green plants can thrive in the absence of light.

Experiments often raise more questions than they answer. New approaches to the problem under consideration as well as desirable new lines of inquiry are constantly opening up to the alert investigator. In this way experimentation leads to more experimentation, more facts accumulate, and more theories are proposed. Some of the suggested hypotheses are confirmed, others are rejected, and still others are modified. Most of them, sound or fallacious, in turn suggest further observation and experimentation. As a result of such endless and painstaking labors there is slowly built up that vast, complex, and ever-changing body of knowledge which we refer to as a science.

The system of subjecting all hypothetical explanations of natural phenomena to experimentation is the essence of experimental science. Progressive modification of accepted concepts in the light of new experimental findings continually increases the soundness of scientific generalizations. Thus there are incorporated into any science theories and generalizations in various stages of acceptance. Some stand upon such a firm substructure of facts that they are accepted by all authorities in the field. Others, less securely supported by experimental results, are subscribed to by some but rejected by other workers. Finally, in any science there are always some theories which are so dubious that they find only a few advocates. Furthermore, some of the theories now widely held sooner or later will be discarded or modified as a result of new findings or as a consequence of different interpretations of facts already known.

However, not all scientists are always in agreement regarding the interpretation of the same sets of facts. Although this state of affairs is entirely consistent with the spirit of scientific research, it is frequently puzzling to students and laymen. Differences of opinion regarding the hypotheses which suitably explain scientific phenomena are most likely to arise when experimental data are inadequate. Disagreements regarding the interpretation of experiments and observations are often inevitable steps in the clarification of scientific generalizations. Controversies usually focus attention upon gaps in our factual information. Frequently, therefore, they are stimulating to research and often lead to a further enrichment of human knowledge.

Without the knowledge of plant processes which has been slowly accumulated through more than two centuries of observation, experimentation, and critical evaluation by numerous workers in all parts of the world, this book could never have been written. In spite of the patient labors of these many workers, vast gaps still exist in our understanding of the physiology of plants—gaps which are reflected in the necessarily inadequate treatment of many topics in this book. The future of this science and all others lies in the hands of the front-line investigators who wage a continual struggle for the extension of human knowledge.

SUGGESTED FOR COLLATERAL READING

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II

PROPERTIES OF SOLUTIONS

Water is the most abundant compound present in all physiologically active plant cells. The water which occurs in a liquid state in plant cells invariably contains other substances dissolved in it and usually also contains dispersed particles which are not in true solution. When the particles dispersed throughout the water are within a certain range of sizes the system of water plus particles falls into the category of *colloidal systems*. The complicated dynamics of living systems can be largely interpreted in terms of the physicochemical properties of solutions and colloidal systems, one component of which is water, although it should not be inferred that nonaqueous solutions and colloidal systems are entirely absent in living organisms.

Similarly liquid water never occurs in the pure state in the natural environment of living organisms. The water of streams, lakes, and oceans invariably contains various substances in solution and usually in the form of dispersed particles as well. This is likewise true of the soil water. Even raindrops, the products of natural distillation, contain gases and other solutes which have dissolved in them from the atmosphere.

General Nature of Solutions.—Simple solutions are systems in which one component (the solute) is dispersed throughout the other (the solvent) in the form of molecules or ions. Theoretically the solvent may be a gas, a solid, or a liquid, but solutions in which the solvent is a liquid are by far the most important in living organisms. Except in extremely concentrated solutions the average distance between the solute particles is usually very great relative to their size. Naturally occurring solutions, whether in living organisms or their environment, usually contain a number of different solutes and are often exceedingly complex. Water is the commonest and most important of all solvents both in the inorganic world and in the realm of living organisms. The further discussion will be principally in terms of aqueous solutions.

Solutions of a Gas in a Liquid.—The water present in living organisms usually contains dissolved gases. Those most commonly present are carbon dioxide, oxygen, and nitrogen. Practically all the water in the environment of organisms—in oceans, lakes, streams, soils, and raindrops—also contains these gases in solution, and sometimes others as well.

A given volume of water or any other liquid will hold only a limited quantity of gas in solution at a given temperature. When no more of a certain gas can be dissolved in a liquid it is said to be *saturated* with respect to that gas. Gases vary widely in their solubility in water, but in general fall into two groups: those which are sparingly soluble, and those which are highly soluble. When only a small fraction of a unit volume of a gas will dissolve in a unit volume of water the gas is classified in the sparingly soluble group. When from one to many unit volumes of a gas will dissolve in one unit volume of water it is classified in the highly soluble group.

Oxygen, hydrogen, and nitrogen are familiar examples of gases belonging to the first group, while carbon dioxide, ammonia, and hydrogen chloride are examples of the second. When gases are highly soluble in water it is usually evidence that a chemical reaction takes place between the gas and water. The reactions between water and carbon dioxide and water and ammonia are indicated in the following equations:

$$CO_2 + H_2O \rightleftarrows H_2CO_3$$

$$NH_3 + H_2O \rightleftarrows NH_4OH$$

In a solution of such gases not only are molecules of the gas present, but also molecules of a compound formed by the reaction of the gas with water. The apparently great solubility of gases such as these results from the formation of relatively soluble compounds by the reaction of the gas with the water. The solubilities of some common gases in water are shown in Table 1.

In general, as also shown in Table 1, an increase in temperature decreases the solubility of a gas in a liquid.

Increase in pressure of a gas above a liquid increases the solubility, *i.e.*, the concentration of that gas in the liquid. For sparingly soluble gases the increase in solubility is directly proportional to the increase in pressure ("Law of Henry"). This principle also holds qualitatively, but not quantitatively, for the very soluble gases.

When a mixture of several gases is maintained over water, each dissolves independently and in accordance with the gaseous pressure ("partial pressure") which it exerts against the surface of the water ("Law of Dalton"). This principle holds strictly only for those gases which are slightly soluble in water. For example, about one-fifth of the atmospheric pressure results from the oxygen present. Assuming an atmospheric pressure of 760 mm. Hg (the value at standard conditions), the pressure resulting from the oxygen is equivalent to about 152 mm. Hg. The quantity of oxygen which dissolves in water exposed to the air is the same as that which would dissolve if oxygen only at a pressure of 152 mm. Hg occupied the space over the water.

TABLE I—SOLUBILITY OF SOME COMMON GASES IN WATER AT DIFFERENT TEMPERATURES WHEN THE PRESSURE OF THE GAS IS ONE ATMOSPHERE

Gas	Volume of gas dissolved in one volume of water (reduced to standard conditions)		
	10° C.	20° C.	30° C.
Carbon Dioxide	1.194	0.878	0.665
Oxygen	0.0380	0.0310	0.0261
Nitrogen	0.0186	0.0154	0.0134
Hydrogen	0.0195	0.0182	0.0170

Solutions of a Liquid in a Liquid.—In general, solutions of a liquid in a liquid fall into two classes: those in which the liquids are freely miscible with each other in all proportions, and those in which each liquid reaches a definite point of saturation in the other. Ethanol (ethyl alcohol) and water, for example, mix with each other in all proportions; such a solution is an example of the first mentioned type. Many oily liquids also are miscible with each other in all proportions. A familiar example is the solution of lubricating oil in gasoline. In solutions of this kind the liquid present in excess is usually considered to be the solvent. In a 50 per cent solution of ethanol and water, either liquid could be considered the solvent, or either could be considered the solute.

Ether, chloroform, and many other liquids are sparingly soluble in water. After water and ether, for example, are shaken together in a flask, two distinct layers of liquid separate upon standing. The upper layer consists of the lighter ether, saturated with water, and the lower consists of water saturated with ether. In both layers, however, the concentration of solute present at saturation is small. In the upper layer ether is the solvent, water the solute; the opposite is true of the lower layer.

Solutions of a Solid in a Liquid.—This is by far the most familiar type