# Introductory Plant Physiology

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*Library of Congress Cataloging in Publication Data*

Noggle, Glen Ray, (date)
Introductory plant physiology.

(Prentice-Hall biological sciences series)
Includes bibliographies and index.
1. Plant physiology. I. Fritz, George John, (date) joint author. II. Title. [DNLM: 1. Plants —Physiology. QK711.2 N776i]
QK711.2.N63 581.1 75-44357
ISBN 0-13-502187-1



10 9 8 7 6 5 4 3 2 1

Printed in the United States of America

Prentice-Hall International, Inc., *London*
Prentice-Hall of Australia Pty. Limited, *Sydney*
Prentice-Hall of Canada, Ltd., *Toronto*
Prentice-Hall of India Private Limited, *New Delhi*
Prentice-Hall of Japan, Inc., *Tokyo*
Prentice-Hall of Southeast Asia Pte. Ltd., *Singapore*

# Preface

This book originated as a course in plant physiology for undergraduate students interested in higher plants and how they grow. Many of the students were majors in forestry, crop science, soil science, horticulture, or pest management and had a variety of backgrounds and training. The course also has served as an introduction to botanical science for students who had a one-semester course in general biology. They had completed one year of college chemistry, but most had no experience with biochemistry or physics. With these students in mind we have attempted to write a book suitable for use in a one-semester course in plant physiology emphasizing higher green plants and the concept of "whole plant" physiology.

The table of contents indicates our view of the important major topics of contemporary plant physiology. While each chapter is organized around several subheadings, the chapters have not been divided into small units. Rather we have tried to make each chapter a reasonably complete and unified account of a major topic or concept. Complete documentation is not included in the text, but a reading list is provided at the end of each chapter. The references are of two kinds: general writings—usually textbooks, monographs, or reviews—and research papers bearing on the material discussed in the chapter. These references will provide access to the current literature of plant physiology.

Each of the authors was responsible for certain chapters—these are identified in the table of contents. We read and criticized each other's work but did not settle on a single style of writing or arrive at complete agreement on all the material covered. Some topics reflect the special interests or interpretation of the authors. In all cases we reminded ourselves continually that we were writing an introductory book for undergraduate students with the background mentioned in the first paragraph.

All the chapters were read at various stages by colleagues and students. Their comments and suggestions were helpful. Special thanks are extended to C. C. Black, Jr., R. D. Dresdner, L. A. Garrard, E. B. Knipling, B. L. Lowenhaupt, J. A. McArthur, J. T. Mullins, J. E. Pallas, Jr., T. O. Perry, E. J. Stadelmann, and J. R. Troyer. We hope that readers will take the opportunity to send us their ideas as to how the book can be improved. Many people gave us permission to use illustrations, photographs, tables, and graphs. They are acknowledged in the text. Finally, we thank our friends and families, who encouraged us during the writing of this book.

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# Contents*



*Chapters 2, 3, 6, 7, 15, 16, 17, 18, and 19 were contributed by G. Ray Noggle. Chapters 1, 4, 5, 8, 9, 10, 11, 12, 13, and 14 were contributed by George J. Fritz.

# 1 Introduction

The higher vascular plants that cover the land areas of the earth have a crucial role in man's existence and survival. They furnish him with food. They provide his livestock with forage. They supply the air he breathes with oxygen. From them he obtains fibers for clothing, wood for shelter and furnishings, and medicines which he uses to alleviate his ailments.

Not only man's primary biological needs but many of the things which he uses in everyday life are obtained from higher vascular plants. [The term *higher vascular plants* refers to those plants that produce seeds (i.e., gymnosperms and angiosperms)]. Included among the useful items obtained from these plants are paper; rubber; spices; nonalcoholic beverages such as tea, cocoa, and coffee; and alcoholic beverages such as wine, beer, whiskey, gin, and vodka. Moreover, higher vascular plants minister to the aesthetic needs of man by beautifying his physical environment. In fact, these plants are the most prominent feature of the natural green landscape.

The fact that man is completely and absolutely dependent on higher vascular plants for the necessities of life makes it imperative that he gain as thorough a knowledge as possible of the science of plant physiology. Moreover, a knowledge of plant physiology is essential to all fields of applied botany, whether agronomy, floriculture, forestry, horticulture, landscape gardening, plant breeding, plant pathology, or pharmacognosy. All these applied sciences depend on plant physiology for information regarding how plants grow and develop.

## THE SCIENCE OF PLANT PHYSIOLOGY

Plant physiology is a study of natural phenomena in living plants. It is the science concerned with processes and functions, the responses of plants to changes in the environment, and the growth and development which result from the responses.

By *process* is meant a natural continuing sequence of events. Examples of processes which occur in living plants are photosynthesis, respiration, ion absorption, translocation, stomatal opening and closing, assimilation, transpiration, flowering, and seed formation. One of the tasks of plant physiology is to describe and explain plant processes. By *function* is meant the natural activity of a thing, whether cell, tissue, organ, chemical substance, or whatever. A second task of plant physiology is to describe and explain the function of each kind of organ, tissue, cell, and cellular organelle in plants and also the function of each chemical constituent, whether ion, molecule, or macromolecule. But since processes and functions are dependent on and modified by external factors such as light and temperature, a third task of plant physiology is to describe and explain how processes and functions respond to changes in the environment. In essence, the overall goal of plant physiology is to evolve a detailed and comprehensive knowledge of all the natural phenomena which occur in living plants and thereby to understand the nature of plant growth and development.

The methods used in plant physiology are derived mainly from chemistry and physics. In fact, an important feature in the development of modern plant physiology has been the increasing role of chemistry and physics in furnishing new ideas and new tools, not only for the solution of old problems but also for the recognition of new ones. Of course it will be realized that processes and functions cannot be understood properly unless something is known about the structures with which they are associated. Therefore some knowledge of plant anatomy, in addition to chemistry and physics, is needed in the study of plant physiology.

The tools used in the study of plant physiology are varied and include all of those traditionally associated with chemistry, physics, and plant anatomy as well as many of the more sophisticated ones developed in recent years. Examples of the latter are chromatography, electron scanning microscopy, electrophoresis, freeze etching, mass spectrometry, and radioactive tracer techniques. In addition, many of the tools distinctively associated with cell biology are used in plant physiology. For example, maceration techniques have made it possible to extract soluble and particulate fractions from plant cells and to study metabolic reactions carried on by individual enzymes and by cellular organelles such as mitochondria, chloroplasts, ribosomes, and nuclei. As a result, an enormous amount of information concerning cellular activities has been gathered during the past several decades. Thus our understanding of the biochemical reactions that occur in plants and the functional significance of cellular organelles has been broadened considerably. It should be kept in mind, however, that individual components of cells operate under more subtle conditions *in vivo* (i.e., in the living condition) than *in vitro* (i.e., when separated from living cells). When organized cellular structure is destroyed and the various parts of the cell are separated the unique capabilities conferred upon a cell by the organized arrangement of interacting components will be impaired.

The science of plant physiology is never static but always changing as new facts are discovered and fresh concepts are developed. It is only natural that plant physiologists may not always have the same opinion regarding the mechanism of certain plant processes or the function of certain plant constituents. Just as two cameras placed at two different points and both trained on the same scene can result in an overall picture which is slightly out of focus, so it is possible for two plant physiologists to reach different conclusions on the basis of a given set of experimental data. The theory proposed by one is challenged by others. However, as more and more data are collected, old interpretations are sifted, weighed, and reexamined in the light of these new data, and new interpretations more in harmony with the known facts of the physiology of plants come into focus. The close interweaving of experimentation and interpretation is a guarantee that progress in understanding will be made. Plant physiology is a self-correcting body of knowledge. Through continuing research efforts and the enfolding of new evidence new ideas come to be known and replace the old.

## PRACTICAL ASPECTS OF PLANT PHYSIOLOGY

Quite apart from the considerable theoretical significance of plant physiology in helping man to understand the world in which he lives, plant physiology serves as the foundation for the numerous recent advances in agriculture, forestry, pharmacology, plant pathology, and other fields of applied botany.

Plant physiology also promises to assume an increasingly important role in agricultural research programs in the near future. As world demand for food increases with rising population, mankind faces enormously complex problems. Their solutions will require input from many sources: social, economic, technological, and agricultural. One of the primary agricultural tasks of the future will be to increase crop production substantially throughout the world. Future agricultural research programs will continue, as in the present, to have as their major goals the production of new and better varieties and strains of crop plants; the improvement of plant protection against insects, diseases, and weeds; the control of soil fertility; and an increase in mechanization efficiency. But in addition there will be a sharp intensification of agricultural and food research. These intensified efforts will lead to demands on plant physiologists not only to supply basic information regarding how plants grow and develop but also to undertake research programs designed specifically to increase crop yields.

There are many aspects of practical agriculture which can be benefited by more intensive research efforts in plant physiology. Only a few will be mentioned here. The efficiency of photosynthetic conversion of solar radiation in the production of food nutrients that are acceptable to human diets can be increased. Better ways to utilize information regarding biological nitrogen fixation will result in increased utilization of nitrogen by plants. Techniques of tissue culture developed during the past several years by plant physiologists can be refined to decrease the time required to create desirable strains of crop plants. Crop yields can be increased by learning how and when the application of plant growth regulators to plants is most effective. Losses of water from plants by transpiration can be minimized by increasing the efficiency of water use. The growth and development of certain crops can be regulated by artificial means of irradiation. The quality of human food nutrients in field and vegetable crops can be regulated through suitable micronutrient additions to soils. The exact growth conditions necessary for optimum yields of crop plants can be determined precisely by growing them in controlled environments (phytotrons). Now useless weeds and jungle plants can be converted to high-quality animal fodder by the addition of fats and proteins produced through large-scale culture of algal and yeast cells.

## HEREDITARY AND ENVIRONMENTAL INFLUENCES ON PLANT BEHAVIOR

It is a basic principle of plant physiology that two sets of factors, hereditary and environmental, regulate the internal processes and conditions of the plant and thereby determine plant growth and development (see Figure 1).

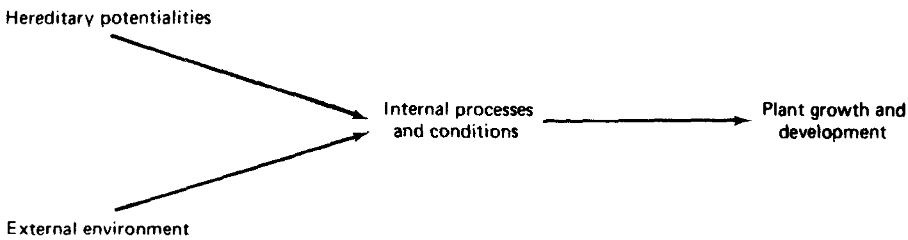


**Figure 1.** Two sets of factors, hereditary and environmental, determine internal processes and conditions in the plant (i.e., the physiology of the plant). Internal processes and conditions, in turn, are expressed in plant growth and development.

Thus the ultimate shape, size, form, and degree of complexity of a plant are the result of the interaction between its genetic composition and the environment in which it grew. Just as the genetic composition of petunia seeds will ensure that they always produce petunia plants, not zinnias or roses, so the environmental factors will determine whether the petunia plants are vigorous or stunted, bright green or yellowish, or turgid or wilted. Modifications caused by variations in environmental factors normally are not inherited.

The information of heredity that "tells" a plant how to behave is determined by the nucleic acids present in all cells of the plant body. Deoxyribonucleic acid (DNA) is the primary genetic substance that conveys hereditary information from generation to generation. How the genetic "blueprint" is transmitted is described in Chapter 3.

Since much of the science of plant physiology is concerned with plant responses to the physical environment, it will be useful, for purposes of orientation, to make a few comments regarding each of the major factors of the physical environment.

The quality, intensity, and duration of radiation which impinges on plants has profound effects on many physiological processes. For example, light affects chlorophyll formation (Chapter 6), photosynthesis (Chapter 7), and photorespiration (Chapter 8). Moreover, light induces cylindrical plant organs (e.g., stems, petioles, coleoptiles) to grow at unequal rates when they are differentially illuminated on the two sides; this phenomenon is referred to as phototropism (Chapter 16). Also, alternations in light and dark periods from day to night (photoperiodicity) control many aspects of plant growth and development [e.g., flower formation and germination of light-sensitive seeds (Chapters 17 and 19)].

The critical importance of soil moisture supply and atmospheric humidity on plant growth and development is recognized by everyone. When a plant does not receive sufficient water or when transpiration rates are excessive its leaves wilt, its growth slows down or ceases altogether, and it may even die (Chapter 14).

Not only water but also a host of chemicals naturally present in the soil and atmosphere affect the growth and development of plants. Mineral ions are supplied by the soil to roots (Chapter 9). Also the gases oxygen and carbon dioxide are vital components of the physical environment. All plant cells require oxygen for respiration (Chapter 4). Carbon dioxide is assimilated in photosynthesis by green leaves in the light (Chapter 7). Oxygen inhibits the magnitude of net photosynthesis in many plants by stimulating a process known as photorespiration (Chapter 8). In addition to naturally occurring chemicals, certain industrial and automobile waste products, both gaseous and particulate, pollute the atmosphere in many geographic areas and pose a special hazard to plants.

The temperature of the soil and air affects not only the rates of physiological processes (e.g., photosynthesis, ion absorption, growth) but also may determine the course of development in plants. Only three examples will be given here. (1) Seeds of certain species will not germinate unless they are exposed to low temperatures for several weeks or months; during this period, certain biochemical changes occur which result in the breaking of dormancy (Chapter 17). (2) In a number of species, exposing the seed to low temperatures for a prolonged period of time results in a hastening of the subsequent flowering of the plants. Similarly, many deciduous trees will not produce flower buds unless subjected to low winter temperatures; this phenomenon