Physiology of Woody Plants

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Preface

This book was written for use as a text by students and teachers and as a reference by investigators and others who desire a better understanding of how trees grow. It should be useful to a wide range of people, including arborists, foresters, horticulturists, plant physiologists, ecologists, and even those who merely wish to know more about trees. It is difficult to write for such a varied audience because of the wide differences in their knowledge and interests. However, it must be assumed that users will have some knowledge of elementary botany and physiology. Nevertheless, we realize that some readers may find parts of the book too technical, while others may find the same sections too elementary. We started with the assumption that it is necessary to understand how trees grow in order to grow trees efficiently. Therefore, we remind those practical people who find some sections rather technical and theoretical that it is necessary to introduce some biochemistry in order to understand physiological processes, such as photosynthesis and respiration, which play essential roles in tree growth. On the other hand, those who find some sections rather elementary are reminded that this book was written primarily for foresters and horticulturists rather than for specialists in plant physiology. This volume is intended to explain how physiological processes are involved in growth of woody plants and how they are affected by the environment, in addition to explaining the mechanisms of the processes themselves.

The viewpoint of this book is somewhat different from that in most textbooks of plant physiology because it places strong emphasis on tree structure and on the interactions of trees and stands of trees with their environment. Considerable attention is devoted to environmental physiology, that is, to the effects of environmental factors on physiological processes. Thus our approach is more ecological than biochemical, although it is made clear that environmental factors operate at the cellular and molecular level. For example, light and temperature affect photosynthesis at the cellular level by affecting guard cell behavior and at the molecular level through effects on the biochemical and biophysical processes occurring in the chloroplasts. There also are repeated references to the internal control systems that regulate and coordinate growth of various tissues and organs and rates of various processes, producing the harmonious combination of structure and function necessary for a plant to thrive.

We emphasize the close interrelationship between structure and function because it is impossible to understand the processes of a plant without understanding its structure. Furthermore, the structure of a tree comes into existence as the result of a complex series of physiological processes that are too often hidden behind the term "growth." We have therefore given considerable attention to structure and the processes by which the various tissues and organs of trees are produced. Vegetative and sexual reproduction are discussed in detail, both because they are important and because they illustrate interesting and important physiological processes.

This book represents a revision, expansion, and updating of two earlier books, "Physiology of Trees" and the two-volume "Growth and Development of Woody Plants." In this volume attention is given to the physiology of ornamental woody plants as well as forest and orchard trees. Readers should understand that the same general physiological processes operate in all kinds of woody and herbaceous plants.

A list of general references has been placed at the end of each chapter and papers cited in the text are listed in the Bibliography at the end of the book. We have attempted to present significant reference material from the world literature so as to make the work authoritative and well documented. Many references refer to recent work but some refer to older work, either because they are interesting historically or because they provide data not available from more recent work. The number of research publications has increased tremendously in the two decades since "Physiology of Trees" was written. It therefore was possible to cite only a fraction of the relevant literature, and we have omitted many important papers. In spite of the great increase in research and publication there is a lack of definitive information on many important topics and much uncertainty about some. Contrasting views have sometimes been presented and in many instances we have given our personal interpretations of the available information. We caution readers that as new information is acquired some conclusions will need to be revised, and we hope that readers will be ready to modify their views when changes become necessary.

In the text, common names are generally used for well-known species and Latin names for less common ones. A list of scientific names and common names of species, when available, is given following the text. Names of North American forest trees are based on E. L. Little's 'Check List of Native and Naturalized Trees of the United States," Agriculture Handbook No. 41, U.S. Forest Service, Washington, D.C. (1953). Names of other species are from various sources.

We express our appreciation for the contributions of the many people who assisted directly and indirectly in the preparation of this book. Much information and stimulation came from our graduate students and from foresters, plant physiologists, and horticulturists all over the world with whom we have worked and discussed problems. We also express our appreciation to the Atomic Energy Commission, the National Science Foundation, the Fulbright Commission, the Food and Agriculture Organization of the United Nations, the U.S. Department of Agriculture, the International Society of Arboriculture, the Wisconsin Department of Natural Resources, the School of Natural Resources and Graduate School of the University of Wisconsin, and the Department of Botany of Duke University, as well as other agencies that financed our research and travel. The senior author also wishes to acknowledge the role of the late C. F. Korstian who first directed his attention to the need for research in the field of tree physiology.

The entire manuscript was read by Henry Hellmers and various chapters were read by R. S. Alberte, R. H. Burris, D. I. Dickmann, J. P. Helgeson, W. Lopushinsky, P. E. Marshall, A. W. Naylor, S. G. Pallardy, R. P. Pharis, C. W. Ralston, J. N. Siedow, E. L. Stone, and B. R. Strain. Their helpful suggestions are greatly appreciated. However, the text has gone through various revisions since they read it, and they should not be held responsible for any errors that may occur. Others who assisted in preparation of the manuscript include J. Buriel, K. Henning, R. C. Koeppen, T. L. Noland, and M. Peet. S. G. Pallardy assisted in preparation of the Index.

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The Role of Plant Physiology

INTRODUCTION

This book describes how trees grow, in contrast to books on silviculture and horticulture which describe how to grow trees. It deals with the physiology of woody plants of all sizes. However, because of their large size, long life, and low ratio of photosynthetic to nonphotosynthetic tissue, trees present special problems and will be used most frequently as examples. Nevertheless, the basic physiological processes are similar in all seed plants so what is said about trees applies to shrubs if adjustments are made for differences in size and length of life.

Trees have different meanings for different people. For our ancestors they were a source of fuel and shelter and sometimes an object of worship. To the home owner they are a source of pleasant shade in the summer, but in the autumn a nuisance which shed leaves on the lawn. Wood was once the chief source of fuel and, as other fuels become scarcer, trees may again become an important renewable source of fuel. To the arborist trees are ornamental objects in the landscape; to conservationists and sportsmen they protect watersheds and game and provide recreation; to the foresters they are a source of timber and pulpwood; and to horticulturists they are a means of producing fruit. To physiologists, however, trees are complex biochemical factories which grow from seeds and literally build themselves. Physiologists are therefore interested in the numerous metabolic processes that collectively produce what we term "growth."

The magnitude of the synthetic process occurring in trees is emphasized by the fact that a hectare (2.47 acres) of temperate zone forest produces about 20 metric tons of dry matter annually, and a hectare of tropical rain forest as much as 100 tons. Readers are warned that these numbers refer to gross, not net, productivity; the latter being much lower, as will be seen in Table 6.1 and in Kira (1975). All of this material is produced from relatively simple raw materials: water, carbon dioxide, and a few kilograms of nitrogen and mineral salts. Thus the success of trees and other green plants depends on their efficiency in manufacturing carbohydrates, nitrogen-containing compounds, and lipids and converting them into new plant tissue. However, growth involves much more than a series of synthetic processes. There must be absorption of sufficient water and mineral nutrients, translocation of organic and inorganic substances to growing regions, and control systems which correlate the numerous processes. This book attempts to explain how these processes occur, how they are affected by the environment and by cultural practices, and how all of these interacting factors affect the quantity and quality of growth.

Plant physiologists are primarily interested in learning how trees grow, while arborists, foresters, and horticulturists are interested primarily in how to grow trees efficiently. The two objectives are more closely related than generally supposed because in order to grow trees efficiently one must understand the basic physiological processes which control growth and how they are affected by environmental factors and cultural processes. Thus basic physiological research can contribute to silvicultural and horticultural research and vice versa. The greatest overall progress will occur when physiologists learn more about how trees grow while foresters and horticulturalists learn more about the physiology of trees, and the two groups cooperate to solve the problems of growing trees as efficiently as possible.

THE ROLE OF PLANT PHYSIOLOGY

The general role of plant physiology is to explain how plants grow and respond to environmental factors and cultural treatments in terms of their physiological processes and conditions. Study of processes such as photosynthesis, translocation, assimilation, respiration, and transpiration may seem far removed from the practice of forestry or horticulture. However, growth is the result of the interaction of physiological processes, and in order to understand why trees grow differently in various environments and with different cultural treatments it is necessary to understand the nature of these physiological processes and how they are affected by the environment.

Nearly everyone knows that the growth of trees, like that of all other organisms, is controlled by their inherited genetic potentialities and their environment, but too little consideration is given to the means by which this control is exerted. To say that shade or drought reduces growth, or that a new combination of genes is responsible for rapid growth of a hybrid, does not really explain how the observed effects are brought about. We need a better understanding of how various causes produce their respective effects. The following diagram shows how heredity and environment interact through the internal physiological processes and conditions of trees to control the quantity and quality of growth. It also shows the relationships among several fields of science which are involved in the study of these phenomena.

Hereditary Potentialities
- The field of genetics
- Selection and breeding programs
- Potential rate of growth, size and longevity of trees
- Type of xylem, depth and extent of root systems

Environmental Factors
- The field of ecology, soil science, climatology, meteorology, etc.
- Radiation, temperature, minerals, competition, pests, silvicultural practices, etc.

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Physiological Processes and Conditions
- The field of plant physiology
- Photosynthesis, carbohydrate and nitrogen metabolism
- Respiration, translocation
- Plant water balance and its effects on growth and metabolism,
- Growth regulators, etc.

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Quantity and Quality of Growth
- The field of arboriculture, forestry, and horticulture
- Amount and quality of wood, fruit, or seed produced
- Vegetative versus reproductive growth
  - Root versus shoot growth

Klebs's Concept

This scheme sometimes is called Klebs's concept because the German plant physiologist Klebs (1913, 1914) was one of the first to point out that environmental factors can affect plant processes only by changing internal processes and conditions. Lundegardh (1931) also made important contributions to this viewpoint. Klebs's concept emphasizes the basic biological principle that the only way in which heredity or environment can affect the growth of an organism is by affecting its internal processes and conditions. The physiological processes of a tree constitute the machinery through which heredity and environment operate to control growth. Therefore, in order to understand why trees are affected by any particular factor or treatment, we must learn how that factor or treatment affects their physiological processes.

Applications of Klebs's Concept

The application of this concept can be illustrated by some specific examples. For instance, if a hybrid grows faster than its parents in the same environment it is because a new combination of genes has produced a more efficient balance of physiological processes, resulting in more food being converted into plant tissue. This may result from increased efficiency of structures or processes, or both. The rate of photosynthesis per unit of leaf area might be increased by increased chlorophyll content, or by structural changes which increase the intake of carbon dioxide or by better exposure of leaves to light. A more extensive root system or a thicker layer of cutin might result in maintenance of a higher level of turgidity in the tree, which in turn would be favorable for photosynthesis and also for cell enlargement.

If a certain slash pine produces more gum than its neighbors in the same environment, this probably is caused by a different genetic constitution resulting in higher rates of those processes which cause food to be converted into gum. Another possibility is that structural differences increase the rate of gum flow. If one species exhibits greater cold or drought resistance or greater shade tolerance than another, it is because its genetic constitution produces differences in structures and or processes which result in more resistance to unfavorable environmental conditions.

Even though a change in rate of growth can be attributed to some structural modification, basically it is dependent on a change in processes. Structures are the products of biochemical processes included in the complex of physiological processes involved in growth, and changes in structure result from changes in processes. Thus processes control structure even though they also are modified by changes in structure.

Unfavorable environmental conditions reduce tree growth because they interfere with various essential physiological processes. For example, water deficits reduce growth because they cause closure of stomata, reduction in photosynthesis, loss of turgidity, cessation of cell enlargement, and other unfavorable conditions within the tree. A deficiency of nitrogen reduces growth because nitrogen is an essential constituent of the proteins required for formation of new protoplasm, enzymes, and other essential substances. Phosphorus, potassium, calcium, sulfur, and other mineral elements are essential because they function as constituents of various structures of essential compounds such as coenzymes, in buffer systems, and in other biochemical systems essential for proper functioning of various physiological processes.

Attacks by insects and fungi reduce tree growth or cause death only when the injury severely interferes with one or more physiological processes. Defoliation of a tree does not reduce growth directly, but does so indirectly by reducing the amount of photosynthesis and synthesis of growth regulators in the crown. If the phloem is attacked, injury to the tree results from decreased translocation of food and growth regulators to the roots, and damage to the root system is harmful to the tree because it reduces the absorption of water and nutrients from the soil. Pathologists and entomologists sometimes have been too much concerned with the description and classification of the causal organisms and have tended to overlook the fact that they were really dealing with physiological problems. Resistance to attacks of insects and fungi is largely biochemical in nature, and injury is the result of disturbance of biochemical and physiological processes. Just as the control of human diseases has progressed enormously through the use of biochemical and physiological approaches, so will the control of tree diseases become more successful as entomologists and pathologists become more aware of the physiological aspects of the problem, instead of merely describing organisms and applying sprays.

We repeat for the sake of emphasis that the only way in which genetic differences, environmental factors, cultural practices, and diseases and insects can affect tree growth is by affecting their internal physiological processes and conditions. The operations of arborists, foresters, and horticulturists should be aimed at producing the most favorable genotypes and environments possible for the operation of the physiological machinery which really controls growth. To do this effectively and efficiently they must understand the nature of the principal physiological processes, their roles in growth, and their reactions to various environmental factors.

THE SCOPE OF TREE PHYSIOLOGY

As Huber (1937) stated, trees have always been regarded by nonbotanists as representing the apex of development in the plant kingdom. Because of their size and beauty they have often been credited with a special personality and have even been worshipped. The peculiar characteristics of trees are a matter of degree rather than of kind, however. They go through the same stages of growth and carry on the same processes as other seed plants, but their larger size, slower maturity, and longer life accentuate certain problems as compared with smaller plants having a shorter life span. The most obvious difference between trees and herbaceous plants is the greater distance over which water, minerals, and food must be translocated and the larger percentage of nonphotosynthetic tissue in trees. Also, because of their longer life span, they usually are exposed to greater variations and extremes of temperature and other climatic and soil conditions than annuals or biennials. Thus, just as trees are notable for their large size, they are also notable for their special physiological problems.

Some Important Physiological Processes and Conditions

The successful growth of trees depends on the interaction of a large number of processes and conditions. Some of the more important physiological processes and the chapters in which they are discussed are listed below:

Photosynthesis: the synthesis of carbohydrates from carbon dioxide and water, by which the chlorophyllous tissue of trees provides the basic food materials for other processes (see Chapter 5)

Nitrogen metabolism: the incorporation of inorganic nitrogen into organic compounds, making possible the synthesis of proteins and protoplasm itself (see Chapter 9)

Lipid or fat metabolism: synthesis of lipids and related compounds (see Chapter 8)

Respiration: the oxidation of food in living cells, releasing the energy used in assimilation, mineral absorption, and other energy-using processes (see Chapter 6)

Assimilation: the conversion of food into new protoplasm, cell walls, and other substances; a basic process in growth (see Chapter 6)

Accumulation of food: the storage of food in seeds and in the parenchyma cells of the wood and bark (see Chapter 7)

Accumulation of salt: the concentration of salt in cells and tissues by an active transport mechanism dependent on the expenditure of metabolic energy (see Chapter 10)

Absorption: the intake of water and minerals from the soil and oxygen and carbon dioxide from the air (see Chapters 5, 10, and 13)

Translocation: the movement of water, minerals, foods, and hormones from place to place in trees (see Chapter 11)

Transpiration: the loss of water in the form of vapor (see Chapter 12)

Growth: permanent increase in size, resulting from the interaction of the various processes listed above (see Chapter 3)

Reproduction: production of cones or flowers, and fruits and seeds; this also results from the interaction of a number of physiological processes

Vegetative reproduction: plays an important role in some species (see Chapter 4)

Growth regulation: the complex interaction of hormones and nutritional balance (see Chapters 15 and 16).

Some of the important physiological conditions affecting growth are as follows:

Amount and efficiency of chlorophyll (see Chapter 5)

Kinds and amounts of carbohydrates present and their interconversion, for example, change of starch to sugar and the reverse (see Chapter 7)

Kinds and amounts of nitrogen compounds and the ratio of carbohydrates to nitrogen (see Chapter 9)

Kinds and amounts of other constituents, such as fats (see Chapters 6 and 8)

Protoplasmic characteristics: cold and drought resistance probably are at least partly dependent on special characteristics of protoplasm (see Chapter 16)

Osmotic pressure of cell sap: increased osmotic pressure is often associated with exposure to drought and cold (see Chapter 14)

Turgidity of cells: loss of turgidity causes cessation of growth and affects rates of various physiological processes (see Chapters 13 and 16)

To physiologists belongs the task of measuring these conditions and processes, studying their mechanisms, observing their reaction to various environmental conditions, and identifying their role in tree growth. The more physiologists can learn about the mechanisms of the principal physiological processes, the better they can assist foresters and horticulturists in solving their practical problems. If we knew enough